

Current Status of the Ferns and Lycophytes of the Hawaiian Islands

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ABSTRACT.—The Hawaiian Islands are well known for having one of the highest documented percentages of endemic plants in the world. Hawaiian ferns and lycophytes represent a relatively large percentage of the endemic flora with approximately 74% of the native fern and lycophyte species considered endemic. In addition, at least 40 taxa are naturalized aliens. We present a new synopsis of the Hawaiian fern and lycophyte flora that includes new state and island records, recent taxonomic updates and problems, and a summary of known and hypothesized geographical origins of fern and lycophyte lineages. We also provide a checklist and access to an interactive key to the native and naturalized ferns and lycophytes of the Hawaiian Islands (<http://www.herbarium.hawaii.edu/lucid/ferns/introduction.html>).

KEY WORDS.—Hawaii, fern, lycophyte, checklist, interactive key

There are 159 native species of ferns and lycophytes in the Hawaiian Islands. Although these represent only about 15% of the native vascular plant flora of the islands (159 fern and lycophyte species: 1032 flowering plant species) (W. L. Wagner, pers. comm. and W. L. Wagner *et al.*, 2005–), fern species are often common components of the vegetation of many mesic to wet plant communities and are sometimes the dominant species both in numbers of individuals and in total biomass (e.g., see Gagné and Cuddihy, 1999). In addition to the native fern and lycophyte taxa, there are now 40 introduced and naturalized taxa, some of which are becoming invasive. Thus, an accurate knowledge of fern and lycophyte diversity in the Hawaiian Islands is important for both basic ecological and evolutionary studies and for conservation management purposes. During the course of preparing an interactive, online key to the ferns of the Hawaiian Islands (see: <http://www.herbarium.hawaii.edu/lucid/ferns/introduction.html>), we conducted a thorough review and analysis of the taxonomic history of Hawaiian ferns and lycophytes. We present here a summary of those studies, including the history of collecting, an overview of fern and lycophyte diversity in the islands, estimates of the geographical origins of native Hawaiian fern and lycophyte lineages, additions to the known flora since the publication of the last floristic inventory (Palmer, 2003), and recent taxonomic changes.

Synopsis of Hawaiian Fern and Lycophyte Floras and Enumerations

It was upon Captain James Cook's voyage of the *HMS Resolution* in 1778 that the first collections of Hawaiian plants were made by the naturalist William Anderson (W. L. Wagner *et al.*, 1999). Anderson made a single collection,

Argemone glauca Pope, and noted 22 plant taxa occurring on the island of Kaua'i. The following year, David Nelson, an apprentice botanist aboard Cook's *Resolution* sister ship the *Discovery*, collected approximately 136 vascular plant specimens (St. John, 1978; W. L. Wagner *et al.*, 1999). Although the ship made excursions to Ni'ihau, Kaua'i, Maui, and Hawai'i, Nelson was able to explore only the island of Hawai'i. The specimens from these voyages are housed at the Natural History Museum in London. Archibald Menzies and Albert Chamisso also were early collectors of Hawaiian plants. Menzies explored five of the Hawaiian Islands from 1788 to 1794 (W. L. Wagner *et al.*, 1999). Chamisso collected in the 1810s on O'ahu and later published species descriptions in the journal *Linnaea* (Robinson, 1912a).

Charles Gaudichaud was the botanist aboard Louis de Freycinet's voyage of the *Uranie* that explored O'ahu, Maui, and Hawai'i for twenty days in 1819, although only seven days were spent on land (St. John and Titcomb, 1983). Gaudichaud collected 4,175 specimens throughout the journey (1817–1820), but unfortunately 2,500 of those were lost in a shipwreck. In 1826, he published his account of Hawaiian ferns and lycophytes in *Botanique du Voyage autour du monde* (Gaudichaud, 1826). He included descriptions for 52 genera and 268 species of ferns and lycophytes. Of these, 17 genera and 37 species were from the Hawaiian Islands.

Between 1825 and 1834, James Macrae, George T. Lay, and David Douglas made collections of Hawaiian ferns and lycophytes (Robinson, 1912a; W. L. Wagner *et al.*, 1999). The botanist William Brackenridge visited the Hawaiian Islands from 1840–1841, as part of the United States Exploring Expedition under the command of Charles Wilkes (W. L. Wagner *et al.*, 1999). Throughout the expedition, he recorded numerous ferns and lycophytes and published brief descriptions for all species, and he also included 46 plates with detailed illustrations (Brackenridge, 1971). Unfortunately the majority of the copies of this publication were destroyed in a fire and only 12 copies were salvaged (Robinson, 1912a). Images of Brackenridge's plates may be viewed at the Smithsonian Institution Libraries website: http://www.sil.si.edu/imagegalaxy/imageGalaxy_MoreImages.cfm?book_id=19-24a.

Several enumerations and diagnostic keys of Hawaiian ferns were made between 1864 and 1887. William T. Brigham and Horace Mann visited Kaua'i, O'ahu, Maui, Moloka'i, and Hawai'i and made a checklist of 113 fern species (Robinson, 1912a). John M. Lydgate (1873) published a synopsis of Hawaiian ferns that included descriptions of 24 genera and keys to 111 taxa. Derby (1875) published a checklist that included 124 fern and 15 lycophyte taxa. Several years later, Edward Bailey (1883) wrote a summary of the Hawaiian ferns that included 149 species, each with descriptions and several with elevational and habitat data, although no identification keys were included. Lorenzo G. Yates (1887) published an enumeration of Hawaiian ferns (129 species) that lacked species descriptions, but which incorporated some habitat and elevational information for most species.

William Hillebrand (1888) spent 20 years in the Hawaiian Islands working as a physician and developing his skills as a botanist. At the time of his death in

1886, part of his manuscript of "The Flora of the Hawaiian Islands" was with the printer. It was not until 1888 that the flora was published. The flora contains generic and specific keys and detailed descriptions for flowering plants, ferns, and lycophytes, including distributional and ethnobotanical information. Hillebrand recognized 29 fern genera with 140 species and two lycophyte genera with 15 species. He also acknowledged numerous varieties (approximately 50 fern and four lycophyte varieties) with the majority occurring within *Asplenium* species.

In 1890, A. B. Lyons created a diagnostic key to the Hawaiian ferns that included a key to genera and species, but he did not include species descriptions. Lyons included 27 genera and 143 taxa (139 species, three varieties, and one undetermined species) (Lyons, 1890). Seven years later, Amos A. Heller (1897) published a report of his observations of plants of the Hawaiian Islands. He provided brief descriptions for 106 fern and lycophyte taxa, including six newly described species, and illustrations for two species. Winifred J. Robinson published four papers over the course of three years (1912–1914) that included keys and detailed descriptions to the families, genera, and species of Hawaiian ferns and lycophytes. She recognized more genera and species than any previous treatment: 43 genera and 166 species of ferns and lycophytes (Robinson, 1912a, 1912b, 1913, 1914). Her treatment included numerous plates of photographs of herbarium specimens along with species descriptions that included synonyms, type localities, distribution, and ethnobotanical uses. Copeland published two papers in which he described several new species and updated the nomenclature for fern collections he received from M. L'abbé Faurie (1914) and Joseph F. Rock (1916).

Several years later, Vaughan MacCaughey focused on the ecological relationships of Hawaiian ferns and lycophytes, and recognized 44 genera and 190 species (MacCaughey, 1918). Carl Christensen revised the nomenclature of the Hawaiian ferns and lycophytes to follow his *Index Filicum* (1906). He published a checklist that accepted 41 genera with 159 fern and lycophyte taxa (Christensen, 1925). Although he did not include identification keys, he did provide additional notes on some species and groups that are in need of further study.

Robert L. Fowler (1940) created an annotated checklist of the ferns and lycophytes of the Kilauea-Mauna Loa section of Hawai'i Volcanoes National Park. His list included six lycophyte species and 60 fern taxa; some taxa included information on where they could be located within the park. In 1952, Douglass H. Hubbard created a booklet of the most common ferns of Hawai'i National Park that included images for 63 species and brief descriptions of the genera. From 1932 to 1980, Otto and Isa Degener published a series of loose-leaf books on the Hawaiian vascular plant flora (Degener, 1932–1980). Their publications include generic and species descriptions and keys, distributional information, and numerous illustrations for 94 fern and 14 lycophyte taxa. During the 1980s Warren H. Wagner Jr. published two papers in the *Fiddlehead Forum* that briefly described the status of the Hawaiian ferns and lycophytes, based on years of field experience by himself and Florence

S. Wagner. In 1981, he presented a checklist of approximately 180 fern and lycophyte taxa (W. H. Wagner, 1981). Seven years later he reported 198 taxa, 172 native (118 endemic) and 26 naturalized, although he acknowledged uncertainties about the exact total number of taxa (W. H. Wagner, 1988).

The two most recent Hawaiian fern and lycophyte floras are from Kathy Valier (1995) and Daniel D. Palmer (2003). Valier did not treat all the Hawaiian ferns and lycophytes, but rather provided descriptions for 61 of the most commonly encountered taxa. She reported, in accordance with W. H. Wagner (1988), about 200 fern and lycophyte taxa, 172 being native. The most up-to-date and comprehensive Hawaiian fern and lycophyte flora is that of Palmer (2003), which included descriptions of fern and lycophyte families, genera, and species along with keys to genera and species and numerous illustrations. Palmer recognized 73 genera and 221 taxa (including hybrids) of Hawaiian ferns and lycophytes. The species descriptions highlight characters that separate each species from similar species and include information on synonyms, current distribution, habitat, elevation, ethnobotanical knowledge, and vernacular names. Palmer was able to record the variability found throughout Hawaiian ferns and lycophytes by observing numerous specimens in the field and in herbaria and including first-hand observations of many type specimens.

Current Treatment

The Hawaiian Islands have representatives from all major lineages of monilophytes except the Equisetopsida and from all three lineages of lycophytes. The endemic fern genera of the Hawaiian Islands have long been thought to consist of *Adenophorus* (Polypodiaceae), *Diellia* (Aspleniaceae), and *Sadleria* (Blechnaceae). [N.B. Authorities for all Hawaiian taxa are given in Appendix 1.] However, molecular work by Schneider *et al.* (2004a, 2005) supported *Diellia* as a monophyletic clade nested within *Asplenium* (Aspleniaceae), therefore decreasing the number of endemic fern genera to two. This classification is recognized in the majority of recent treatments (Christenhusz *et al.*, 2011; Smith *et al.*, 2006, 2008; Snow *et al.*, 2011; Viane and Reichstein, 1991). There are presently 144 native fern species (167 taxa) and 15 native lycophyte species (16 taxa), not including hybrids in the Hawaiian Islands. The genera with the most Hawaiian fern taxa are *Asplenium* (29 taxa), *Dryopteris* (20 taxa), and *Adenophorus* (12 taxa). A synopsis of the statistics of the Hawaiian fern and lycophyte flora is given in Table 1.

New Fern Records in the Hawaiian Islands

Several new state and island records of native and naturalized ferns have been published since Palmer's flora (2003), including seven new state records of naturalized ferns (Table 2). In addition, 20 new island records have been reported, most of which are also naturalized ferns. One new island record of a native species is of the endemic *Asplenium haleakalense*, which was

TABLE 1. Current statistics for the ferns and lycophytes of the Hawaiian Islands¹.

	Ferns	Lycophytes	Total ferns and lycophytes
Families	25	3	28
Endemic genera	2	0	2
Genera with all naturalized species	16	0	16
Indigenous genera	48	5	53
Native genera	50	5	55
Total genera	66	5	71
Endemic species	110	7	117
Indigenous species	34	8	42
Total native species	144	15	159
Endemic hybrids	18	6	24
Indigenous hybrids	0	0	0
Total native hybrids	18	6	24
Endemic taxa *	132	8	140
Indigenous taxa *	35	8	43
Total native taxa *	167	16	183
Naturalized species	33	3	36
Naturalized taxa *	37	3	40
Total native and naturalized species	177	18	195
Total native and naturalized taxa *	204	19	223
Total native and naturalized taxa **	222	25	247

¹ includes species presumed extinct
* includes subspecies, varieties, and cultivars, but does not include forms or hybrids
** includes subspecies, varieties, cultivars, and hybrids

described in 1999 and known previously only from Maui (Palmer, 2003). A specimen at the Herbarium Pacificum (BISH) collected on Hawai'i in 1995 was determined as *A. haleakalense* by Dan Palmer in 2002, thus representing a new island record for this species (Kennedy *et al.*, 2010). *Microlepia speluncae* (Dennstaedtiaceae) is another example of a new island record for a native species. Palmer (2003) reported the species to be distributed on the islands of Kaua'i, O'ahu, and Hawai'i, but it has been documented subsequently on Maui (Oppenheimer, 2003) and Moloka'i (Oppenheimer, 2008).

Four noteworthy rediscoveries include *Asplenium diellaciniatum* (syn. *Diellia laciniata*), *Asplenium dielmannii* (syn. *Diellia mannii*), *Ctenitis squamigera* (Dryopteridaceae), and *Pteris lidgatei* (Pteridaceae) (Table 2). *Asplenium diellaciniatum* was rediscovered on the island of Kaua'i (Wood, 2006). Palmer (2003) recognized this taxon as a form of the federally listed species, *Diellia erecta* (f. *alexandri*), and noted it was likely extinct on Kaua'i. Recent morphological studies by Lorence *et al.* (in press) conclude that *Diellia erecta* f. *alexandri* represents two distinct species with one endemic to Kaua'i (*Asplenium diellaciniatum*) and the other to Maui Nui. In 2004, a population of 49 individuals was discovered on slopes of the Kawai'iki Stream in western Kaua'i (Wood, 2006). The most recent report documents a decline in the population to 39 individuals (USFWS, 2009a). Currently the species is not

TABLE 2. New species, state records, island records, and rediscoveries of ferns and lycophytes in the Hawaiian Islands subsequent to Palmer (2003).

Taxon	Island								Reference
	N	K	O	Mo	L	Ka	Ma	H	
<i>Adiantum</i> 'Edwinii' ^{NZ}			I		x		x		Lau and Frohlich, 2012
<i>Angiopteris evecta</i> ^{NZ}		I	x	I	x		x	x	Oppenheimer, 2010; Wood, 2006
<i>Asplenium diellaciniatum</i> ^N		D							Wood, 2006
<i>Asplenium dielmanni</i> ^N		D					x	I	Agurauja and Wood, 2003
<i>Asplenium haleakalense</i> ^N									Kennedy <i>et al.</i> , 2010
<i>Blechnum orientale</i> ^{NZ}			S						Lau and Frohlich., 2012
<i>Ceratopteris gaudichaudii</i> * ^{NZ}		x	x					I	Imada, 2007
<i>Cheilanthes viridis</i> ^{NZ}		x	x		I		x	x	Oppenheimer, 2007
<i>Ctenitis squamigera</i> ^N		D	x	x	x		x		K. Wood, 2012
<i>Cyclosorus pendens</i> ^N		N	N	N			N	N	Palmer, 2005
<i>Davallia fejeensis</i> ^{NZ}			S				I		Frohlich and Lau, 2008; D. Lorence, pers. comm.
<i>Deparia cataracticola</i> ^N		N							Kato, 2001
<i>Dicksonia fibrosa</i> ^{NZ}								S	Lorence and Flynn, 2006
<i>Diplazium esculentum</i> ^{NZ}		x	x	I	x		x	x	Oppenheimer, 2007
<i>Elaphoglossum paleaceum</i> ^N		x	x	x	I		x	x	Oppenheimer, 2010
<i>Huperzia filiformis</i> ^N		I	x	x	x		x	x	K. Wood, 2012
<i>Lindsaea ensifolia</i> ^{NZ}		x	x	I			x	x	Oppenheimer, 2008
<i>Lygodium japonicum</i> ^{NZ}			x					I	Wilson, 2003
<i>Marsilea minuta</i> ^{NZ}			S						Wilson, 2003
<i>Microlepia speluncae</i> ^N		x	x	I			I	x	Oppenheimer, 2003, 2008
<i>Nephrolepis brownii</i> ^{NZ}	I	x	x	x	x		x	x	Imada, 2007; Wood and LeGrande, 2006
<i>Ophioglossum petiolatum</i> ^N		x	x	I	x		x	x	Oppenheimer, 2010
<i>Phymatosorus scolopendria</i> ^{NZ}							S		Oppenheimer, 2006
<i>Pteris lidgatei</i> ^N			x	D			x		Oppenheimer, 2008
<i>Pteris tremula</i> ^{NZ}							S		Oppenheimer, 2007
<i>Pteris vittata</i> ^{NZ}		x	x	I	I		x	x	Oppenheimer, 2003, 2008
<i>Pyrosia piloselloides</i> ^{NZ}			S						Lau and Frohlich, 2012
<i>Sphaeropteris cooperi</i> ^{NZ}		x	x		I		x	x	Oppenheimer, 2008
<i>Tectaria incisa</i> ^{NZ}		x	x				I	x	Imada, 2007

* var. vulgaris
N native
NZ naturalized

Record abbreviations: N=new species; S=new state record; I=new island record; D=rediscovery; x=previous records (Palmer, 2003); ex=possibly extinct

Island abbreviations: N=Ni'ihau; K=Kaua'i; O=O'ahu; Mo=Moloka'i; L=Lāna'i; Ma=Maui; Ka=Kaho'olawe; H=Hawai'i

federally listed or proposed for listing. As discussed later, the presumed extinct fern, *Asplenium dielmannii*, was also rediscovered on Kaua'i (Aguraju and Wood, 2003).

Another rediscovery on Kaua'i is that of *Ctenitis squamigera*, a species previously known from all main Hawaiian Islands with the exception of Kaho'olawe and Ni'ihau. It was last collected on Kaua'i in the late 1800's and thus presumed extinct on the island until its rediscovery in two separate locations in 2011 (K. Wood, 2012). *Pteris lidgatei* was rediscovered on the island of Moloka'i (Oppenheimer, 2007). Its last known collection on Moloka'i was in 1912, and since then had been considered extinct on the island (Oppenheimer, 2007; Palmer, 2003; W. H. Wagner *et al.*, 1999). On Moloka'i, eight individuals are known from a single population (USFWS, 2009b).

An interesting island record is that of *Psilotum nudum* (Psilotaceae). Although present on all main Hawaiian Islands including Ni'ihau and Kaho'olawe, *P. nudum* was never reported from any Northwestern Hawaiian Island (Palmer, 2003). A collection of *P. nudum* made in 1923 from Midway Atoll was discovered in 2008 in the collections of the Herbarium Pacificum (Kennedy *et al.*, 2010). Two other possible island records, based on herbarium specimens, are of *Doryopteris angelica* (Pteridaceae) and *D. takeuchii*. Yesilyurt (2005) proposed that the endangered Kaua'i endemic, *Doryopteris angelica*, has a more extensive distribution than had been previously reported (Palmer, 2003) occurring on O'ahu, Moloka'i, and Lāna'i. She also determined a range extension for the endangered (USFWS, 2012a) *Doryopteris takeuchii*, to the island of Lāna'i, previously thought to be endemic to Diamond Head Crater on O'ahu. It is imperative to note that Yesilyurt's (2005) conclusions were based on relatively few older herbarium specimens (5 specimens of *D. takeuchii* and 11 specimens of *D. angelica*), and she did not observe the type specimens for either species. For these reasons and because both of these ferns are currently federally listed endangered species it is important that new field observations be made to assess the current distribution of these two species before we accept the range extensions proposed by Yesilyurt (2005).

Newly Described Hawaiian Fern Taxa

Only one native species, *Cyclosorus pendens* (syn. *Pneumatopteris pendens*; Thelypteridaceae), has been described since Palmer's (2003) manual was published (Palmer, 2005). This species is found on Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i at elevations of 368–1220 m and is most similar morphologically to *C. sandwicensis* (Palmer, 2005). Characters that define *C. pendens* are a habitat of damp, mossy rocks often near streams and pendent, lanceolate leaves with obtuse pinnae and rachises and costae that are densely covered with hairs (Palmer, 2005).

Another species not included in Palmer (2003) is *Deparia cataracticola* (Athuriaceae), of which the author was unaware when his book was in press (D. Palmer, pers. comm.). This species is endemic to Kaua'i and is found on wet, mossy cliffs in waterfalls, a habitat similar to where the extinct *D.*

kaalaana was found (Kato, 2001). *Deparia cataracticola* is recognizable by having an ascending to erect rhizome, brown scales at the stipe base, medial sori, leaf blades that are somewhat or not tapered at the base, and by the presence of many proliferations on the lamina (Kato, 2001).

Two species of Hawaiian *Doryopteris* that were not included by Palmer (2003) have recently been recognized. Yesilyurt (2005) recognized six species of *Doryopteris* in the Hawaiian Islands, whereas Palmer (2003) recognized four species and one hybrid. The Hawaiian species of *Doryopteris* are known to have extreme inter- and intraspecific variability, leading to difficulties when circumscribing species (Palmer, 2003; Yesilyurt, 2005). For example, *Doryopteris subdecipiens* was first described by W. H. Wagner *et al.* (1999) who noted that it most likely was the result of hybridization between *D. decipiens* and *D. decora*. Palmer (2003) preferred to recognize *D. subdecipiens* as a hybrid due to its variability of characters and the continuum of intermediates between the putative parental species. The morphological study by Yesilyurt (2005) recognized this entity at the species level, although she did not rule out the possibility of it being of hybrid origin. She did not examine the type specimen and only examined nine herbarium specimens for which she noted much variation (Yesilyurt, 2005). We agree with Palmer (2003) that this species should not be recognized at the species level due to its variability and intermediate characters between the parent species. Another species, *D. tryonii*, was described in 1963 by O. Degener and I. Degener, but later synonymized under *D. decora* by Palmer (2003). Yesilyurt (2005) segregated this species based on its filiform segments, pinnate division, and crenulate indusium margins. Because the Hawaiian *Doryopteris* species exhibit high morphological variation and possibly hybridization, it is unclear whether they represent distinct species. Further studies are needed to clarify species circumscriptions.

Naturalized Hawaiian Fern Taxa

Palmer (2003) reported 33 naturalized fern and lycophyte taxa in the Hawaiian Islands. Since then, seven new state records of naturalized ferns have been reported, including taxa from previously unreported families and genera in the Hawaiian Islands (Table 3). Two previously unreported families include Davalliaceae and Dicksoniaceae, and three previously unreported genera include *Davallia* (Davalliaceae), *Dicksonia* (Dicksoniaceae), and *Pyrrosia* (Polypodiaceae).

Naturalized taxa are found on all eight main Hawaiian Islands, with O'ahu having the majority of naturalized taxa (Figure 1; Table 3). Three naturalized species, *Nephrolepis brownii* (Nephrolepidaceae), *Pityrogramma austroamericana* (Pteridaceae), and *P. calomelanos*, are found on all main Hawaiian Islands. Listed below are the seven recent new state records based on the work of Hank Oppenheimer, Ken Wilson, and the staff at the Hawai'i Biological Survey and the National Tropical Botanical Garden.

TABLE 3. Current distribution of naturalized fern and lycophyte taxa in the Hawaiian Islands.

Taxon	Island							
	N	K	O	Mo	L	Ka	Ma	H
<i>Adiantum</i> ‘Edwinii’			x		x		x	
<i>Adiantum hispidulum</i>		x	x	x	x	x	x	x
<i>Adiantum raddianum</i>		x	x	x	x		x	x
<i>Adiantum tenerum</i>			x				x	
<i>Angiopteris evecta</i>		x	x	x	x		x	x
<i>Azolla filiculoides</i>		x	x	x	x		x	x
<i>Blechnum appendiculatum</i>		x	x	x	x		x	x
<i>Blechnum orientale</i> *			x					
<i>Ceratopteris gaudichaudii</i> var. <i>vulgaris</i>		x	x					x
<i>Cheilanthes viridis</i>		x	x		x		x	x
<i>Cyclosorus dentatus</i>		x	x	x	x		x	x
<i>Cyclosorus parasiticus</i>		x	x	x	x		x	x
<i>Cyrtomium falcatum</i>		x	x	x	x		x	x
<i>Davallia fejeensis</i> *			x				x	
<i>Deparia petersenii</i>		x	x	x	x		x	x
<i>Dicksonia fibrosa</i> *								x
<i>Diplazium esculentum</i>		x	x	x	x		x	x
<i>Lindsaea ensifolia</i>		x	x	x			x	x
<i>Lygodium japonicum</i>			x					x
<i>Macrothelypteris torresiana</i>		x	x				x	x
<i>Marsilea minuta</i> *			x					
<i>Nephrolepis brownii</i>	x	x	x	x	x	x	x	x
<i>Nephrolepis falcata</i> ‘Furcans’		x	x	x	x		x	x
<i>Nephrolepis hirsutula</i> ‘Superba’		x					x	
<i>Phlebodium aureum</i>		x	x	x	x		x	x
<i>Phymatosorus grossus</i>		x	x	x	x		x	x
<i>Phymatosorus scolopendria</i> *							x	
<i>Pityrogramma austroamericana</i>	x	x	x	x	x	x	x	x
<i>Pityrogramma calomelanos</i>	x	x	x	x	x	x	x	x
<i>Platycerium bifurcatum</i>			x				x	x
<i>Platycerium superbum</i>			x					
<i>Pteris tremula</i> *							x	
<i>Pteris vittata</i>		x	x	x	x		x	x
<i>Pyrrosia piloselloides</i> *			x					
<i>Salvinia molesta</i>			x					x
<i>Selaginella kraussiana</i>			x				x	x
<i>Selaginella stellata</i>								x
<i>Selaginella umbrosa</i>								x
<i>Sphaeropteris cooperi</i>		x	x		x		x	x
<i>Tectaria incisa</i>		x	x				x	x

* indicates new state record subsequent to Palmer (2003)
Hawaiian Island abbreviations: N=Ni’ihau; K=Kaua’i; O=O’ahu; Mo=Moloka’i; L=Lāna’i; Ma=Maui; Ka=Kaho’olawe; H=Hawai’i

Blechnum orientale (Blechnaceae) was discovered naturalized in two locations on the island of O’ahu in 2010 (Lau and Frohlich, 2012). It is native to tropical Asia, Australia, and several Pacific Islands (Chambers and Farrant, 2001; Chiou *et al.*, 1994). Diagnostic characters include rhizomes that are short,

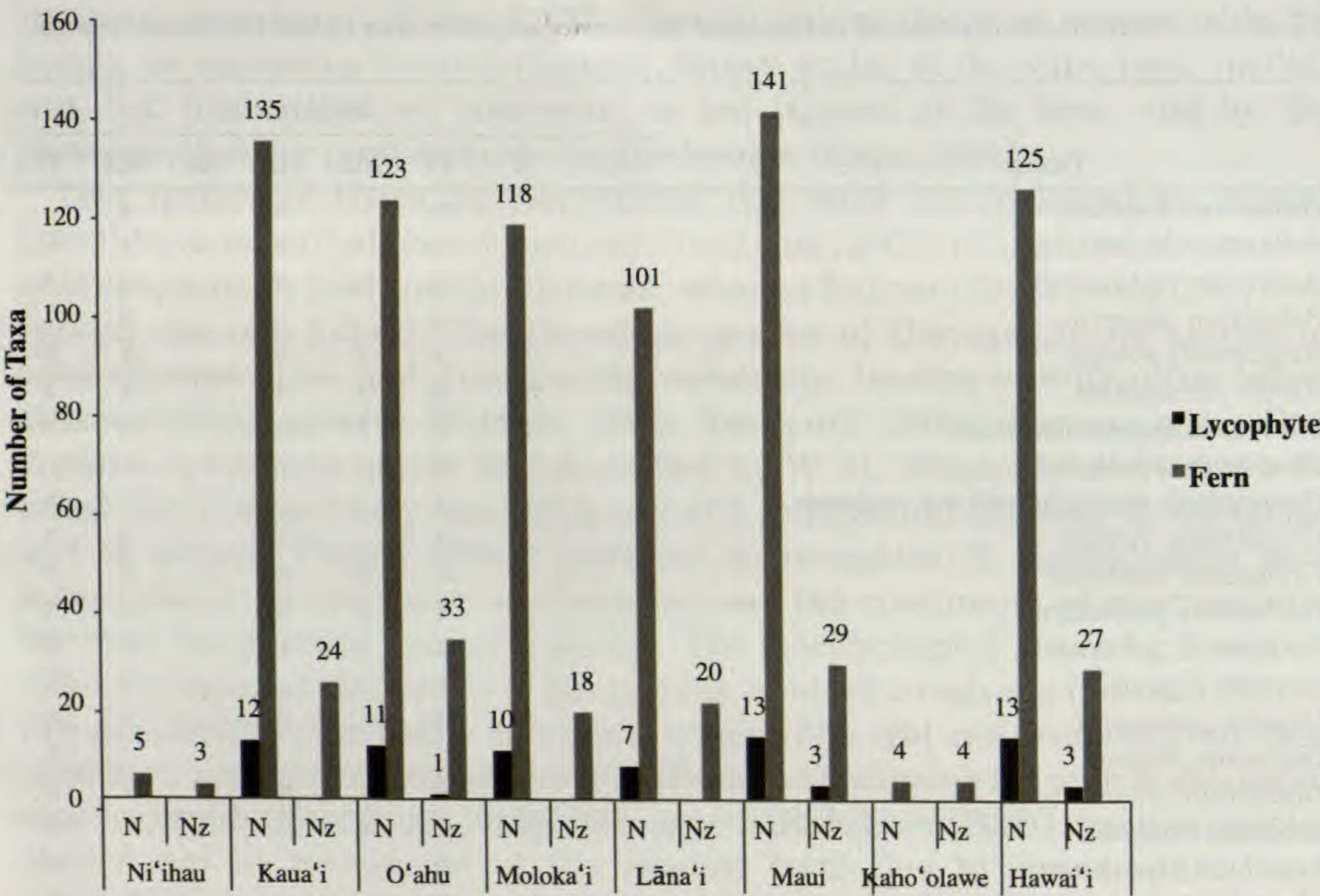


FIG. 1. Native (N) and naturalized (NZ) fern and lycophyte taxa on the eight main Hawaiian Islands. The total taxa per island includes taxa presumed extinct.

erect, and trunk-like; fronds up to 200 cm or more with blades pinnately divided; pinnae 5–30 cm long; and sori that are linear, costal, and indusiate.

Davallia fejeensis (Davalliaceae), a native to the Fiji Islands, was first reported naturalized on O’ahu in 2007 in the Nu’uanu Valley (Frohlich and Lau, 2008). The authors reported *D. fejeensis* as being widely cultivated on O’ahu and likely cultivated on other islands as well. A collection of this species (Lorence 10375, PTBG) was recently made near Haiku in eastern Maui (D. Lorence, pers. comm.). This species is identified by its epiphytic or sometimes terrestrial habitat, creeping rhizomes, blades that are divided 4–5 times with linear ultimate segments bearing a single vein that does not touch the margin, and sori that are solitary at segment tips (Morton, 1957; Nooteboom, 1994).

Dicksonia fibrosa (Dicksoniaceae), a New Zealand native tree fern, was reported naturalized in one locality in the South Hilo district on the island of Hawai’i (Lorence and Flynn, 2006). This species is distinguished from other Hawaiian ferns by trunks that reach 30–60 cm in diameter and up to 6 m tall, stipes with brown hairs, 20–30+ leaves per plant, blades that gradually taper towards the base, and bivalved indusia with the outer valve not differentiated from the lamina (Alan, 1982).

The first record of the aquatic fern *Marsilea minuta* (syn. *M. crenata* (Nagalingum *et al.*, 2007; Whitten *et al.*, 2012)) (Marsileaceae) is puzzling. Hillebrand (1888) reported *M. minuta* (treated as *M. crenulata*) on O’ahu,

preserved in the “Godet herbarium,” although Robinson (1912a) reported that no such herbarium was known. Further investigation into the location of this specimen has been unsuccessful, although other collections from the Godet herbarium have been found at the Botanic Garden and Botanical Museum Berlin-Dahlem herbarium (B). The most recent record of *Marsilea minuta* was made in 1994 when it was found growing in taro patches at the Hawai’i Nature Center in Makiki Valley on O’ahu (Wilson, 2002, 2003). *Marsilea minuta* is native to Africa, Australia, India, and Southeast Asia (Jacona and Johnson, 2006). It is morphologically similar to the endemic *M. villosa*, which also has an aquatic habit, pinnae that are clover-like (divided into four equal pinnae), and sori enclosed in hardened sporocarps located at the bases of long stipes. This naturalized species is readily distinguished from the endemic species by its usually glabrous blades (sometimes with a few scattered hairs) with crenate pinnae margins (entire margins in aquatic forms) (Jacona and Johnson, 2006), in contrast with the glabrous blades and slightly denticulate pinnae margins of *M. villosa* (Johnson, 1986; Palmer, 2003). Furthermore, the naturalized species has roots located at nodes and internodes (Jacona and Johnson, 2006), whereas *M. villosa* has roots restricted to the nodes (Johnson, 1986).

Two populations of *Phymatosorus scolopendria* (Polypodiaceae) were reported on Maui (Oppenheimer, 2006). A collection of this species was made (Oppenheimer & Hansen H80308, BISH), but cannot be located for verification. *Phymatosorus scolopendria* is native to tropical Africa and Asia, Australia, and the Pacific (Brownlie, 1977). This species closely resembles and can easily be mistaken for a common naturalized fern, *P. grossus*, but is distinguished by its epiphytic habit (vs. terrestrial), smaller size, and fewer laminar lobes (Brownlie, 1977).

Pyrrosia piloselloides was found naturalized in a 2–3 acre area in the Woodlawn section of Mānoa Valley on the island of O’ahu in 2010 (Lau and Frohlich, 2012). This species is native to China, India, and Malesia (Ravensberg and Hennipman, 1986). *Pyrrosia piloselloides* is a small, epiphytic, colony-forming fern diagnosable by its sterile succulent leaves reaching 1–7 cm long, fertile linear leaves from 4–16 cm long, and linear, submarginal sori (Hovenkamp, 1986).

Pteris tremula was first reported as naturalized on Maui (Oppenheimer, 2007), when it was noted as becoming widespread throughout the central Kula areas at elevations from 914 to 1220 m. No further report has been found concerning its distributional status in the Hawaiian Islands. This species is native to Australia, New Zealand, and the Fiji Islands; it is identified by its erect leaves that attain one meter in length and blades that are 2–4 times pinnately divided with linear, toothed pinnules (Kramer and McCarthy, 1998).

Taxonomic Updates

Smith *et al.* (2006) revised the familial classification for all extant ferns based on the results of numerous molecular and morphological studies. They recognized 37 families with approximately 265 to 312 genera. A more recent

classification for extant ferns and lycophytes by Christenhusz *et al.* (2011) built upon the classification of Smith *et al.* (2006) with recent phylogenetic studies. Christenhusz *et al.* (2011) recognized 3 families with 5 lycophyte genera and 45 families with approximately 280 fern genera. Snow *et al.* (2011) addressed the need to update the taxonomy and nomenclature of the Hawaiian ferns and lycophytes. Their treatment primarily followed the classification by Smith *et al.* (2006, 2008). Rothfels *et al.* (2012b) reexamined the classification of the Eupolypods II and recognized 10 families with 36 genera. A recent classification of the Lycopodiaceae by Øllgaard (2012) accepts 9 Neotropical genera. Although these publications clarify the classification of extant ferns and lycophytes, it is important to note that many fern and lycophyte genera lack molecular studies and are in need of phylogenetic analyses to assess proposed generic delimitations (Christenhusz *et al.*, 2011; Smith *et al.*, 2006). Below, we summarize recent taxonomic and nomenclatural changes and problems that still require further study for Hawaiian fern taxa.

OPHIOGLOSSACEAE.—One example of fern genera in need of further phylogenetic analysis is within the family Ophioglossaceae. The majority of treatments include *Sceptridium* within the genus *Botrychium*, and *Ophioderma* within *Ophioglossum* (Christenhusz *et al.*, 2011; Smith *et al.*, 2006, 2008). However, a molecular study by Hauk *et al.* (2003), using plastid DNA sequences from *rbcL* and *trnL-F*, showed strong support for the segregation of *Sceptridium* and *Ophioderma* as distinct genera. Snow *et al.* (2011) included *Sceptridium* within *Botrychium* and did not address the segregation of *Ophioderma*. Further phylogenetic analyses are needed to resolve these issues.

BLECHNACEAE.—Another example of uncertain generic boundaries is evident with the circumscription of *Blechnum*, in which Shepherd *et al.* (2007) determined *Blechnum* to be paraphyletic and including *Doodia* and *Sadleria*. In accordance with earlier work by Cranfill (2001), *Sadleria*, an endemic Hawaiian genus, was found nested within *Blechnum*. However, *S. cyatheoides* was the only species of the genus included in the study and its placement had only weak support. Christenhusz *et al.* (2011) accept the genus *Sadleria*, but state that the status is not clear due to *Blechnum* being likely paraphyletic. Rothfels *et al.* (2012b) accept the genus *Sadleria* based on the inferred phylogeny of Rothfels *et al.* (2012a). Strong support was found for *Doodia* as a monophyletic group within *Blechnum* with *B. brasiliense* Desv. as the sister species (Shepherd *et al.*, 2007). Further analyses of *Doodia* are needed before making taxonomic changes because only six of the 15–18 species of *Doodia* were sampled, including only one of the two Hawaiian endemic species (*D. kunthiana*). In addition, only one small region of plastid DNA was sequenced (*trnL-F*) and results differed depending on how the data were analyzed. Furthermore, according to the maximum likelihood tree of Shepherd *et al.* (2007), *Blechnum brasiliense* could be placed within *Doodia* to produce a monophyletic genus. Rothfels *et al.* (2012b) conserve the genus *Doodia*, whereas Christenhusz *et al.* (2011) recognize *Doodia* within the genus *Blechnum*.

ATHYRIACEAE AND CYSTOPTERIDACEAE.—Several recent classifications tentatively place the families Athyriaceae and Cystopteridaceae in Woodsiaceae, which includes four genera found in the Hawaiian Islands: *Athyrium*, *Cystopteris*, *Deparia*, and *Diplazium* (Smith *et al.* 2006, 2008; Snow *et al.*, 2011). Molecular work by Schuettpelz and Pryer (2007), using three plastid genes, revealed two members of the Woodsiaceae, *Gymnocarpium* (not present in the Hawaiian Islands) and *Cystopteris*, to be paraphyletic and sister to the eupolypods II. Based on these findings, the authors suggested that several families be recognized. Christenhusz *et al.* (2011) placed both *Cystopteris* and *Gymnocarpium*, along with two additional genera, into Cystopteridaceae. The remaining Hawaiian genera (*Athyrium*, *Deparia*, and *Diplazium*), placed within Woodsiaceae as circumscribed by Smith *et al.* (2006, 2008), are included in Athyriaceae by Christenhusz *et al.* (2011) and Rothfels *et al.* (2012b). This placement is based on results from several previously published molecular studies (Sano *et al.*, 2000; Schuettpelz and Pryer, 2007; Wang *et al.*, 2003).

NEPHROLEPIDACEAE.—The familial placement of *Nephrolepis* is unresolved. Kramer (1990) and Palmer (2003) recognized *Nephrolepis* in its own monogeneric family, Nephrolepidaceae. Smith *et al.* (2006, 2008) tentatively placed the genus within Lomariopsidaceae, which Snow *et al.* (2011) followed. Recent molecular work using plastid DNA data from three regions revealed strong support for *Cyclopeltis* and *Lomariopsis* as sister to *Nephrolepis* (Hennequin *et al.*, 2010). The authors suggested that *Nephrolepis* should be treated in its own family, Nephrolepidaceae, until further molecular analyses have been made.

POLYPODIACEAE.—Palmer (2003) recognized three Hawaiian genera of Grammitidaceae: *Adenophorus*, *Grammitis*, and *Lellingeria*. Smith *et al.* (2006, 2008) placed the family within the Polypodiaceae to resolve issues of paraphyly when Grammitidaceae is recognized (i.e., grammitid ferns form a clade that is nested within Polypodiaceae; Schneider *et al.*, 2004b). Molecular and morphological studies have shown strong evidence for *Adenophorus* as a monophyletic lineage, with *Grammitis tenella* as the sister taxon to *Adenophorus* (Ranker *et al.*, 2003, 2004). Based on these findings, Ranker (2008) transferred *Grammitis tenella* to *Adenophorus* (*A. tenellus*).

The remaining grammitid genera that include Hawaiian species, *Grammitis* and *Lellingeria*, were found to be polyphyletic (Ranker *et al.*, 2004). Strong support was found for a monophyletic clade within *Grammitis* (*Grammitis* sect. *Grammitis*) that includes the type species of the genus, *G. marginella* Sw. (Ranker *et al.*, 2004), but none of the Hawaiian species. Species within that clade share the unique character of black, sclerified leaf margins, a character not found in Hawaiian *Grammitis* (Bishop, 1977; Ranker *et al.*, 2004). In response to those findings as well as from her observations of morphology, Parris (2007) described five new genera, including reestablishing the genus *Oreogrammitis*, in which she included the three Hawaiian *Grammitis* species. Preliminary data (Ranker *et al.*, unpublished) based on plastid DNA sequences *rbcL*, *atp β* , and *trnL-trnF* found there is inadequate information to determine

the monophyly of *Oreogrammitis*. Work is in progress to further resolve the generic circumscriptions within *Grammitis* s. l. (Sundue *et al.*, unpublished). Thus, the placement of the Hawaiian members of *Grammitis* s. l. is currently unclear, although the Hawaiian species clearly do not belong to *Grammitis* s. s. due to the lack of black, sclerified leaf margins. We treat the Hawaiian species here as within *Oreogrammitis* pending further study.

Ranker *et al.* (2004) found *Lellingeria* to be divided into two non-sister clades: one including the *L. apiculata* (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran and *L. myosuroides* (Sw.) A. R. Sm. & R. C. Moran groups (sister to *Melpomene* A. R. Sm. & R. C. Moran) and the other including the *L. mitchelliae* (Baker) A. R. Sm. & R. C. Moran group, now called *Leucotrichum* Labiak, (sister to *Alansmia* M. Kessler, Moguel, Sundue and Labiak) (Kessler *et al.*, 2011; Rouhan *et al.*, 2012). *Lellingeria saffordii*, the sole Hawaiian representative, is an endemic species that occurs on all major islands except Ni'ihau and Kaho'olawe. It is nested phylogenetically within the *L. myosuroides* group, which has recently been described as the new genus *Stenogrammitis* (Labiak, 2011), and thus the Hawaiian species is treated here as *S. saffordii*.

PTERIDACEAE.—*Ceratopteris* is represented in the Hawaiian Islands only by the naturalized species, *C. thalictroides*, which is found on Kaua'i, O'ahu, and Hawai'i (Imada, 2007; Palmer, 2003). Species in the genus are generally polymorphic and this is especially so with *C. thalictroides* (Masuyama and Watano, 2010). The genus has been variously recognized as including 11 species (e.g., Christensen, 1906), four species (Lloyd, 1974), with Lloyd lumping four previously described species into *C. thalictroides*, and 3 species (Tryon and Tryon, 1982). Masuyama and Watano (2010) proposed that five taxa be segregated from *C. thalictroides* based on differences in the nucleotide sequences of plastid DNA, cytological evidence, and morphological differences (Masuyama *et al.*, 2002; Masuyama and Watano, 2005; Masuyama, 2008). The *Ceratopteris* found in the Hawaiian Islands included a newly described taxon, *C. gaudichaudii* var. *vulgaris*, also known from China, Guam, Japan, Korea, Nepal, and Taiwan (Masuyama and Watano, 2010). Masuyama and Watano (2010) examined two specimens from O'ahu and determined Hawaiian members to be this new variety. Although *C. gaudichaudii* var. *vulgaris* occurs on O'ahu, it is important to note that additional *Ceratopteris* taxa may be present in the Hawaiian Islands; further study is needed.

Distribution

The majority of fern and lycophyte taxa are found on six of the eight main Hawaiian Islands (i.e., Kaua'i, O'ahu, Moloka'i, Lāna'i, Maui, and Hawai'i), with few found on Ni'ihau and Kaho'olawe (Figure 1). Two species, the endemic *Doryopteris decipiens* and the indigenous *Psilotum nudum* are distributed on all eight main Hawaiian Islands. [NB: Indigenous is defined here as taxa that are native to a particular area, but are also native elsewhere.] In total there are 140 endemic fern and lycophyte taxa, representing

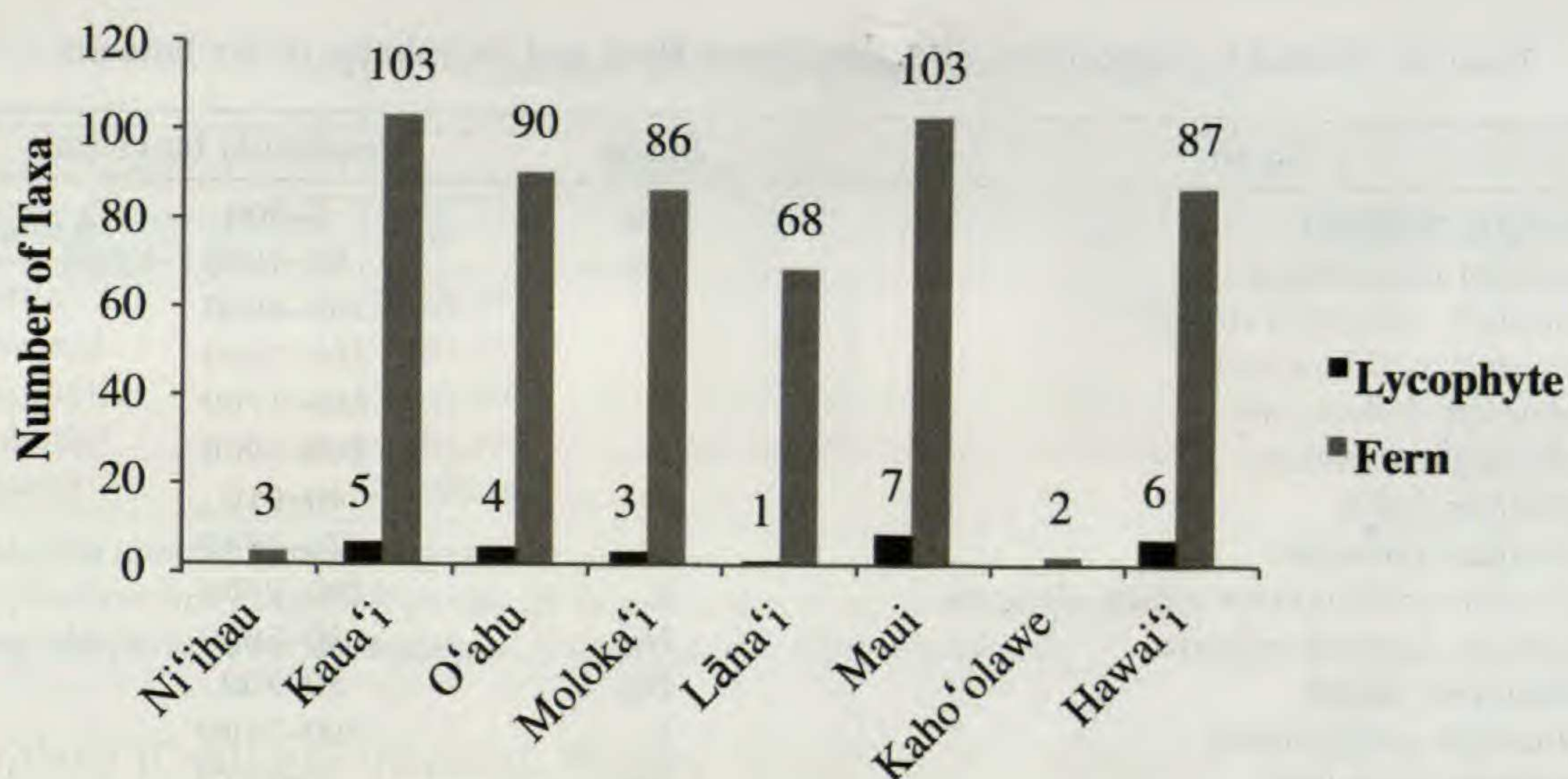


FIG. 2. Endemic fern taxa on each main Hawaiian island. The total taxa per island includes taxa presumed extinct.

approximately 77% of the 183 native taxa. This level of endemism is high compared to other oceanic islands, which usually have endemic rates of less than 50% (Moran, 2008). The greatest numbers of endemic fern and lycophyte taxa are found on Kaua'i and Maui (Figure 2). Despite the high level of island-wide endemism, Hawaiian ferns and lycophytes have relatively low numbers of single-island (28 taxa) and two-island (19 taxa) endemics (Figure 3). Only Kaua'i, O'ahu, and Maui have single-island endemics, with Kaua'i harboring the greatest number (17 taxa). The majority of taxa that are restricted to two islands are found on Maui (15 taxa) and Hawai'i (12 taxa).

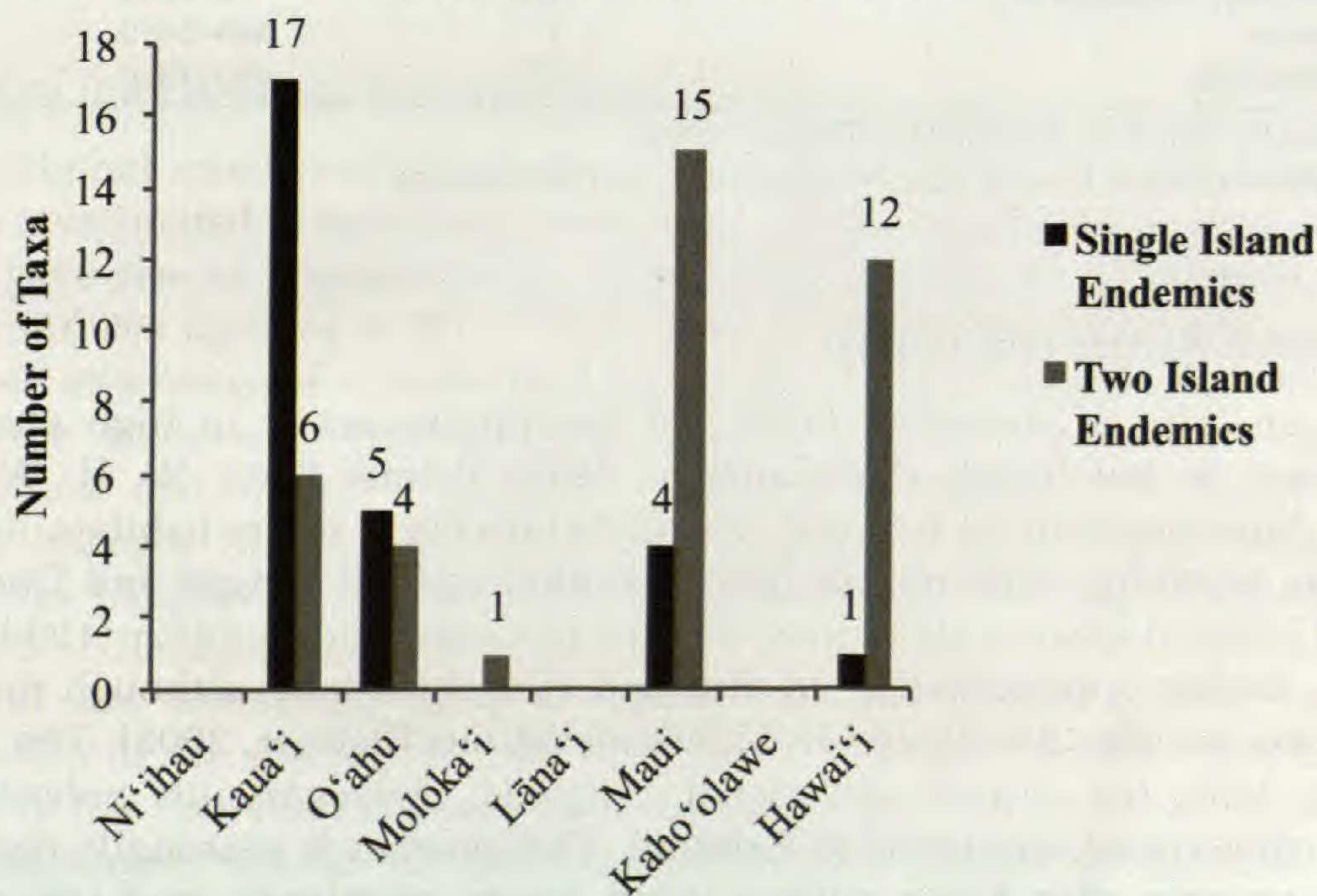


FIG. 3. Distribution of single- and two-island endemics in the eight main Hawaiian Islands. The total taxa per island includes taxa presumed extinct.

TABLE 4. Endemic, indigenous, and naturalized ferns and lycophytes of dry habitats.

Taxon	Status	Elevational range (m)
<i>Adiantum</i> ‘Edwinii’	Nz	0–500
<i>Adiantum hispidulum</i>	Nz	90–1250 (–1825)
<i>Asplenium adiantum-nigrum</i>	I	350–4000
<i>Asplenium aethiopicum</i> *	I	305–1950
<i>Asplenium dielerectum</i>	E	500–1700
<i>Asplenium caudatum</i>	I	200–1000
<i>Asplenium nidus</i>	I	40–610
<i>Asplenium normale</i>	I	375–1680
<i>Asplenium trichomanes</i> subsp. <i>densum</i>	E	1200–2700
<i>Blechnum appendiculatum</i>	Nz	30–560
<i>Cheilanthes viridis</i>	Nz	10–700
<i>Cyrtomium caryotideum</i>	I	300–2100
<i>Cyrtomium falcatum</i>	Nz	0–1525
<i>Doodia kunthiana</i>	E	90–1220
<i>Doryopteris decipiens</i>	E	30–915
<i>Doryopteris decora</i>	E	120–700
<i>Doryopteris takeuchii</i>	E	100–120
<i>Dryopteris fuscoatra</i> var. <i>fuscoatra</i>	E	500–2100
<i>Lepisorus thunbergianus</i>	I	10–2100
<i>Lycopodium venustulum</i> var. <i>verticale</i>	E	1220–2440
<i>Microlepia speluncae</i>	I	480–1280
<i>Microlepia strigosa</i> var. <i>mauiensis</i>	E	0–1770
<i>Microlepia strigosa</i> var. <i>strigosa</i>	I	425–1830
<i>Nephrolepis brownii</i>	Nz	low elevations
<i>Pellaea ternifolia</i>	I	600–3500
<i>Phlebodium aureum</i>	Nz	0–700
<i>Pityrogramma austroamericana</i>	Nz	45–1525
<i>Pityrogramma calomelanos</i>	Nz	0–1000
<i>Pteris cretica</i>	I	340–2450
<i>Pteris irregularis</i>	E	450–1920

*occasionally found in dry habitats (Palmer, 2003)
Status abbreviations: E=endemic; I=indigenous; Nz=naturalized

Elevational Ranges and Habitat

The majority of Hawaiian ferns and lycophytes occur in high elevation mesic-wet to wet forests (MacCaughey, 1918; Palmer 2003; W. H. Wagner, 1995). Approximately 31 fern and lycophyte taxa occur in dry habitats, defined as areas receiving 1200 mm or less of annual rainfall (Gagné and Cuddihy, 1999) (Table 4). Coastal elevations, defined by Gagné and Cuddihy (1999) as 0–300 m, harbor approximately 48 fern and lycophyte taxa, although many of these taxa are also distributed in higher elevations (Palmer, 2003). The native species with the lowest elevational range is *Ophioglossum polyphyllum* (Ophioglossaceae), occurring at 2–160 m. This species is seasonally common, appearing only after heavy rains in sand dunes, grasslands, and lava cobble (Palmer, 2003). Native species that occur at some of the highest elevations (above 3000 m) include: *Asplenium adiantum-nigrum* (Aspleniaceae), *Cystopteris*

TABLE 5. Summary of fern and lycophyte taxa habitats¹.

Habitat	Number of taxa (%)			Total taxa
	E	I	Nz	
Aquatic	2 (28.57)	1 (14.29)	4 (57.14)	7
Terrestrial	117 (62.23)	39 (20.75)	32 (17.02)	188
Lithophytic	23 (63.89)	9 (25.00)	4 (11.11)	36
Epiphytic*	44 (66.67)	15 (22.73)	7 (10.61)	66
Epigeous	3 (100.00)	0	0	3

¹ includes species presumed extinct
* *Vandenboschia davallioides* can be hemi-epiphytic as well as epiphytic
Status abbreviations: E=endemic; I=indigenous; Nz=naturalized

douglasii (Cystopteridaceae), *Pellaea ternifolia* (Pteridaceae), and *Polystichum haleakalense* (Dryopteridaceae).

The majority of Hawaiian ferns are terrestrial, although many are epiphytic and occur mostly in high elevation, wet forests (Table 5). Several species are restricted to aquatic habitats, including the endangered endemic water clover fern, *Marsilea villosa* and the rare lycophyte, *Isoetes hawaiiensis* (Isoëtaceae). Other interesting habitats include those that are epigeous (growing above, but near the surface of the ground in moss mats at the base of trees) and lithophytic/epipetric (growing on rocks). Only three taxa have an epigeous habit, and all are within the endemic genus *Adenophorus*: *A. epigaeus*, *A. tamariscinus* var. *tamariscinus*, and *A. tripinnatifidus*. Several examples of lithophytic species include *Asplenium dielirectum*, *Cyclosorus boydiae*, *C. pendens*, and *Doryopteris takeuchii*.

Origins of the Hawaiian fern and lycophyte flora

The original number of colonizing species of angiosperms to the Hawaiian Islands is estimated to have been a minimum of 291 species (Sakai *et al.*, 1995), which gave rise to approximately 1032 native species (W. L. Wagner, pers. comm. and see updates at W. L. Wagner *et al.*, 2005–) in the flowering plant flora (i.e., an average of ~3.6 derived species per colonizing ancestor). We used data from molecular phylogenetic studies and/or information on the geographical distribution of species and genera to estimate the origins of 78 taxa or lineages (33 endemic and 45 indigenous) of Hawaiian ferns and lycophytes (Appendix 2). Molecular phylogenetic data were available for 22 taxa and/or lineages (see references cited in Appendix 2). We inferred the origin of the remaining 56 taxa and/or lineages based on the current distribution of the species (i.e., for indigenous species of limited distribution outside of the Hawaiian Islands) or of the genus (i.e., for Hawaiian endemics with congeneric species of limited distribution outside of the Hawaiian Islands). The 78 taxa or lineages comprise 103 taxa in total, thus there are an average of ~1.3 extant taxa per inferred colonizing species (Table 6 and Appendix 2). We estimate that the majority of Hawaiian fern and lycophyte

TABLE 6. Estimated source regions for the origins of Hawaiian fern and lycophyte lineages¹.

Distribution of lineage sister to Hawaiian lineage	E (%)	I (%)	N (%)
Asia/Paleotropics	21 (64)	25 (56)	46 (59)
Neotropics/Americas	6 (18)	5 (11)	11 (14)
Boreal	2 (6)	1 (2)	3 (4)
Pantropical	2 (6)	10 (22)	12 (15)
Cosmopolitan	1 (3)	2 (4)	3 (4)
South Pacific	0 (0)	2 (4)	2 (3)
Austral	1 (3)	0 (0)	1 (1)
Total known/estimated	33	45	78
Total unknown	60	0	60

¹ includes species presumed extinct
Status abbreviations: E=endemic; I=indigenous; N= native (endemic + indigenous lineages)

lineages (59%) are of Asian/Paleotropical origin (Table 6); that broad area is the most distant from the Hawaiian Islands compared to other possible source regions. Other hypothesized source regions include Pantropical (15%, but directionality unknown), Americas/Neotropics (14%), Cosmopolitan (4%, but directionality unknown), Boreal (4%), South Pacific (3%), and Austral (1%) (Table 6). Geiger *et al.* (2007 and references therein) identified four climate- or weather-based phenomena that might allow spores to be carried great distances to the Hawaiian Islands: 1) the northern subtropical jet stream from southeast Asia/Malaysia, 2) northern trade winds from America, 3) tropical storms from Mexico and Central America, and 4) a Hadley Cell shift from the tropical convergence zone that would allow for the Marquesas Islands to be a source area (Geiger *et al.*, 2007; Wright *et al.*, 2001).

Many Hawaiian angiosperm genera are believed to be derived from single colonization events with subsequent diversifications, including the Hawaiian silverswords (Asteraceae), *Bidens* (Asteraceae), and *Schiedea* (Caryophyllaceae) (Baldwin and Wagner, 2010). This contrasts with Hawaiian fern genera, which are often the result of multiple colonization events. For example, several biogeographical studies focused on determining the origins of Hawaiian Dryopteridaceae. Geiger and Ranker (2005) used chloroplast DNA (cpDNA) sequences from *rbcL* and *trnL-F* to explore the origins of Hawaiian *Dryopteris* species. They found Hawaiian *Dryopteris* to be the result of multiple colonizations and hypothesized five separate colonization events, most of these likely of Southeast Asian origin. In another study of Dryopteridaceae, Driscoll and Barrington (2007) used the same cpDNA sequences as Geiger and Ranker (2005) to explore the origins of Hawaiian *Polystichum* species. They determined it to be polyphyletic as well, with *P. hillebrandii* being of separate continental eastern Asian origins from the remaining two species, *P. haleakalense* and *P. bonseyi*.

Considerable work also has been conducted to determine the biogeographical origins of the Hawaiian grammitid ferns (*Adenophorus*, *Oreogrammitis* (formerly *Grammitis*, in part), and *Stenogrammitis* (syn. *Lellingeria*)). Ranker

et al. (2004) used cpDNA sequences from *rbcL* and *atp β* to explore the phylogeny of the grammitid ferns. Their results suggested three colonization events to the Hawaiian Islands. Species of the endemic Hawaiian genus *Adenophorus* (10 spp.) were hypothesized to have originated from a single Neotropical ancestor and further analyses from Geiger *et al.* (2007) provided additional support for this hypothesis. The origins of Hawaiian *Oreogrammitis* (3 spp.) are unclear. Ranker *et al.* (2004) postulated a southwest Pacific origin based on the sister relationship of *O. knutsfordiana* (Baker) Parris to the Hawaiian *Oreogrammitis* clade. Geiger *et al.* (2007) further supported this hypothesis, but the exact origins of the Hawaiian clade are unknown due to the widespread distribution of *O. knutsfordiana*. The third genus of Hawaiian grammitids, *Stenogrammitis* (1 sp.), is believed to be of Neotropical origin. Geiger *et al.* (2007) determined the Hawaiian species *S. saffordii* to be sister to *S. subcoriacea* (Copel.) Labiak from the Marquesas and Society Islands. Because this clade is sister to the Neotropical species *S. limula*, they hypothesized a Neotropical origin for the Hawaiian *Stenogrammitis*. A recent study by Labiak *et al.* (2010) suggests a Neotropical origin, but provided support for *S. saffordii* as being sister to the Mexican species *S. hellwigii* (Mickel & Beitel) Labiak.

Multiple colonizations like those for the Dryopteridaceae also have been postulated for Hawaiian *Doryopteris* (Yesilyurt, 2005) and the indigenous *Asplenium adiantum-nigrum* (Ranker *et al.*, 1994; Shivas, 1969). According to Yesilyurt (2005) there are molecular data (Yesilyurt *et al.* in prep) that suggest *D. decora* and *D. decipiens* are the result of separate introductions to the Hawaiian Islands. Another Hawaiian fern, the aquatic *Marsilea villosa*, has been hypothesized to be of North American ancestry. Nagalingum *et al.* (2007) used six plastid regions to determine strong support for *M. villosa* as being sister to *M. oligospora* Goodd. and *M. vestita* Hook. & Grev., both North American temperate species. Molecular work by Whitten *et al.* (2012) found additional support for a North American origin. Shivas (1969) hypothesized *Asplenium adiantum-nigrum* to be of hybrid origin from two diploid European taxa based on cytological data. Ranker *et al.* (1994) used isozyme data to infer multiple colonization events of this species to the Hawaiian Islands.

Conservation of Hawaiian Ferns

Conservation of the Hawaiian flora and preservation of the native forests is of most immediate concern in the Hawaiian Islands. Extinction rates within the United States are highest in the Hawaiian Islands (Gagné, 1988). Despite this high level of extinction, only three historically documented fern species and one lycophyte species are presumed to be extinct in the Hawaiian Islands (Table 7). The primary threat to the decline of Hawaiian ferns and lycophytes is habitat destruction by humans and feral animals (Given, 1993; W. H. Wagner, 1995). Habitat destruction of the Hawaiian Islands began with the Polynesian settlers, but increased rapidly after Western contact (Gagné, 1988). The introduction of feral animals (e.g., pigs, sheep, cattle, deer, goats) and

TABLE 7. Federal and state status of Hawaiian ferns and lycophytes.

Taxon	Date Federally Listed	Status				
		X	E	C	SC	SGCN
<i>Adenophorus periens</i> **	11/10/1994		x			x
<i>Asplenium dielirectum</i> **	11/10/1994		x			x
<i>Asplenium dielfalcatum</i>	10/29/1991		x			x
<i>Asplenium dielmannii</i> **	05/13/2010		x		x	x
<i>Asplenium dielpallidum</i> **	02/25/1994		x			x
<i>Asplenium leucostegioides</i>	-	x			x	
<i>Asplenium peruvianum</i> var. <i>insulare</i> **	09/26/1994		x			x
<i>Asplenium schizophyllum</i>	-				x	
<i>Asplenium unisorum</i>	06/27/1994		x			x
<i>Athyrium microphyllum</i> *	-					x
<i>Cibotium chamissoi</i> *	-					x
<i>Cibotium glaucum</i> *	-					x
<i>Cibotium</i> spp.	-					x
<i>Ctenitis squamigera</i>	09/26/1994		x			x
<i>Cyclosorus boydiae</i>	-			x		
<i>Cyclosorus interruptus</i> *	-					x
<i>Cyclosorus waialele</i>	-				x	
<i>Cystopteris douglasii</i>	-				x	
<i>Deparia kaalaana</i>	-	x			x	
<i>Dicranopteris linearis</i> *	-					x
<i>Diplazium molokaiense</i> **	09/26/1994		x			x
<i>Diplazium sandwichianum</i> *	-					x
<i>Doryopteris angelica</i> **	05/13/2010		x			x
<i>Doryopteris takeuchii</i>	09/18/2012		x			
<i>Dryopteris crinalis</i> var. <i>podosora</i> **	05/13/2010		x		x	x
<i>Dryopteris tetrapinnata</i>	-				x	x
<i>Dryopteris</i> spp.	-					x
<i>Elaphoglossum</i> spp.	-					
<i>Huperzia haleakalae</i> ***	-	x				
<i>Huperzia mannii</i>	05/15/1992		x			x
<i>Huperzia nutans</i>	03/28/1994		x			x
<i>Huperzia stemmermanniae</i> **	-			x		x
<i>Isoetes hawaiiensis</i>	-				x	
<i>Marsilea villosa</i> *	06/22/1992		x			x
<i>Microlepia strigosa</i> var. <i>mauiensis</i>	-			x		x
<i>Pteris lidgatei</i> **	09/26/1994		x			x
<i>Sadleria cyatheoides</i> *	-					x
<i>Sceptridium subbifoliatum</i>	-	x			x	

* important component of native habitat (Mitchell *et al.*, 2005)
** fewer than 50 individuals in the wild (PEP, 2011)
*** extant elsewhere, extinct only in the Hawaiian Islands (W. L. Wagner *et al.*, 2005–)
Status designation: X=extinct (Wagner *et al.*, 2005–); E=endangered (USFWS, 2012a; 2012b); C=candidate (USFWS, 2012b); SC=species of concern (DOFAW, 2001); SGCN =species of greatest conservation need (Mitchell *et al.*, 2005)

non-native plant species has further contributed to the habitat loss and population decline in Hawaiian ferns (W. H. Wagner, 1995).

Approximately 1366 non-native vascular plant species have been introduced to the Hawaiian Islands and have since become naturalized (C. Imada, pers. comm. and W. L. Wagner *et al.*, 2012). These plants were introduced to the Hawaiian Islands primarily for their use in the horticultural trade, although some introductions were accidental. Non-native, alien taxa have the potential to become naturalized and possibly invasive by competing with the native flora. Over 260 species of cultivated alien ferns are estimated to have been introduced to the Hawaiian Islands mainly for the horticultural trade and use in botanical gardens (Robinson *et al.*, 2010; Wilson, 1996). The most recent publications (Palmer, 2003; Wilson, 2002) report 33 naturalized fern and lycophyte taxa, all of which were likely introduced to the islands after 1880 (Wilson, 2002). As stated above, since Palmer (2003) was published, seven new fern taxa have been reported as naturalized in the state (Table 3).

Single, invasive fern species have caused major problems in many parts of the world (Robinson *et al.*, 2010). By contrast, at least 18 species in the Hawaiian Islands have become invasive based on their abundance and widespread distribution throughout the islands (Palmer, 2003). Invasive species often are highly detrimental to native ecosystems due to their ability to outcompete and displace the native flora. For example, the introduced tree fern *Sphaeropteris cooperi* (Cyatheaceae) grows faster and produces more leaves than the native tree ferns, *Cibotium* spp. (Cibotiaceae) (Durand and Goldstein, 2001). Another example is of the common, naturalized fern *Blechnum appendiculatum*, reported as one of the two plants completely overgrowing a population of the endangered fern *Asplenium dielpallidum* (Agurajuja *et al.*, 2004).

Several naturalized fern species hybridize with native Hawaiian species. For example, the naturalized fern *Cyclosorus dentatus* has crossed with the endemic species *Cyclosorus cyatheoides* (*Cyclosorus* \times *palmeri* (W. H. Wagner) W. H. Wagner) on Kaua'i and O'ahu (W. H. Wagner *et al.*, 1999). Another example is of an intergeneric hybrid (\times *Lindsaeosoria flynnii* W. H. Wagner), the naturalized *Lindsaea ensifolia* (Lindsaeaceae) crossing with the indigenous *Sphenomeris chinensis* (Lindsaeaceae) (W. H. Wagner, 1993). The effects of naturalized species crossing with native species are not entirely known, although these hybrids have the potential to threaten native biodiversity due to the effects of outbreeding depression and introgression (Bleeker *et al.*, 2007).

Many Hawaiian endemic ferns are difficult to cultivate, likely because of their requirement of highly specialized habitats (W. H. Wagner, 1995). Examples of this are ferns with green spores (grammitid ferns and Hymenophyllaceae) that germinate immediately, given the proper environmental factors (Mehltreter, 2010). However, if proper environmental conditions are not met, the chlorophyll in the spores can quickly break down, and viability of the spores may be reduced to approximately seven weeks (Mehltreter, 2010). Propagation of these ferns can be difficult and expensive due to the need for specific environmental conditions that are not always

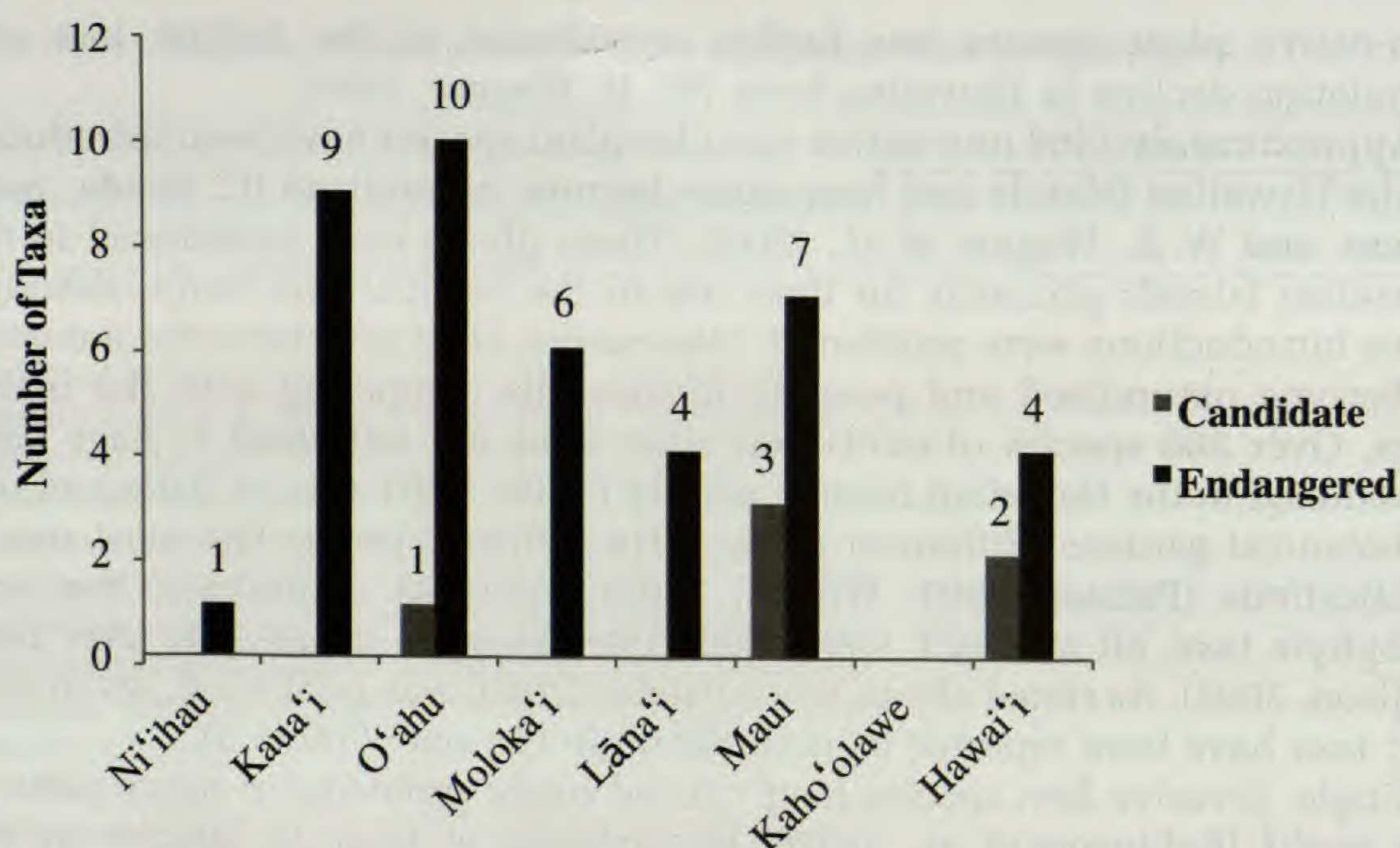


FIG. 4. Federally listed endangered, proposed, and candidate taxa on each of the main Hawaiian Islands. The total taxa per island includes taxa presumed extinct.

achievable in the traditional greenhouse settings (W. H. Wagner, 1995). It is therefore critical that these species are identified so accurate environmental assessments are documented and land be preserved that can host these endemic species.

Endangered Hawaiian Ferns

As of 2012, the U. S. Fish and Wildlife Service had listed 339 Hawaiian plant taxa as either threatened (9 taxa) or endangered (330 taxa). Of those, 5% are ferns (14 taxa) and lycophytes (2 taxa) and all are listed as endangered (Table 7). *Doryopteris takeuchii*, a fern endemic to Diamond Head Crater on O'ahu, was recently listed as endangered (USFWS, 2012a). In addition, three taxa are candidate species: *Cyclosorus boydiae*, *Microlepia strigosa* var. *mauiensis*, and *Huperzia stemmermanniae* (Lycopodiaceae). The greatest number of federally listed (including endangered and candidate taxa) ferns and lycophytes occur on O'ahu, although Kaua'i and Maui have nearly the same number (Figure 4). One taxon, *Dryopteris glabra* var. *pusilla*, was formerly listed as a candidate species, but has been removed due to the likelihood that the species has a greater distribution than previously thought; additional surveys are needed (USFWS, 2004).

The Hawai'i Department of Fish and Wildlife (DOFAW, 2001) identified nine fern taxa and one lycophyte as "species of concern" and in greatest need of conservation efforts (Table 7). W. L. Wagner *et al.* (2005–) consider three of these to be extinct (i.e., *Asplenium leucostegioides*, *Deparia kaalaana*, and *Sceptridium subbifoliatum* (Ophioglossaceae)) and two are currently federally listed as endangered (*Asplenium dielmannii* and *Dryopteris crinalis* var. *podosora*).

TABLE 8. Reported individuals of federally listed endangered Hawaiian ferns and lycophytes in wild populations.

Taxon	Reported individuals	Reference
<i>Adenophorus periens</i>	15–123	USFWS, 2010a
<i>Asplenium dielirectum</i>	<100	USFWS, 2009c
<i>Asplenium dielfalcatum</i>	thousands	USFWS, 2011a
<i>Asplenium dielmannii</i>	~60	K. Wood, pers. comm.
<i>Asplenium dielpallidum</i>	12	USFWS, 2008
<i>Asplenium peruvianum</i> var. <i>insulare</i>	278	USFWS, 1998
<i>Asplenium unisorum</i>	1148	USFWS, 2011b
<i>Ctenitis squamigera</i>	234–242	USFWS, 2009d
<i>Diplazium molokaiense</i>	~65	USFWS, 2010b
<i>Doryopteris angelica</i>	29–54	USFWS, 2011c
<i>Doryopteris takeuchii</i>	50–100	USFWS, 2012a
<i>Dryopteris crinalis</i> var. <i>podosora</i>	32–47	USFWS, 2011d
<i>Huperzia mannii</i>	61–71	USFWS, 2011e
<i>Huperzia nutans</i>	11	USFWS, 2009e
<i>Marsilea villosa</i>	thousands	USFWS, 2011f
<i>Pteris lidgatei</i>	51	USFWS, 2009b

In 2005, DOFAW and the Division of Aquatic Resources (DAR) within the Department of Land and Natural Resources (DLNR) developed a Comprehensive Wildlife Conservation Strategy (CWCS) to review the status of the native terrestrial and aquatic species in the Hawaiian Islands (Mitchell *et al.*, 2005). The CWCS identifies the Hawaiian species of greatest conservation need (SGCN) and provides strategic plans for their conservation. The criteria CWCS used to determine a SGCN need may be found at: http://www.state.hi.us/dlnr/dofaw/cwcs/process_strategy.htm. The CWCS includes 22 ferns and 3 lycophytes as species of greatest conservation need (Table 7). Eight of these species are listed as SGCN because they play an important role in their native habitats as either a dominant member of the native plant community or by hosting or providing habitat for other native species (Mitchell *et al.*, 2005). Along with these species, three genera (*Cibotium*, *Dryopteris*, and *Elaphoglossum*) also have this designation (Mitchell *et al.*, 2005).

The Plant Extinction Prevention (PEP) program of Hawai'i reported nine fern taxa and one lycophyte with less than 50 individuals remaining in wild populations: *Adenophorus periens*, *Asplenium dielirectum*, *A. dielmannii*, *A. dielpallidum*, *Asplenium peruvianum* var. *insulare*, *Diplazium molokaiense*, *Doryopteris angelica*, *Dryopteris crinalis* var. *podosora*, *Huperzia stemmermanniae*, and *Pteris lidgatei* (PEP, 2011). Approximate numbers of currently known individuals of endangered Hawaiian ferns have been compiled from reports of the USFWS and additional resources (Table 8).

Extinct Hawaiian Ferns

W. L. Wagner *et al.* (2005–) reported three ferns and one lycophyte from the Hawaiian Islands as extinct (Table 7). A single plant of one previously

believed extinct species (HBS, 1999), *Asplenium dielmannii* (syn. *Diellia mannii*), was rediscovered on Kaua'i in 2003 (Agurajuja and Wood, 2003). Prior to this discovery, the last known collections were made in western Kaua'i sometime between 1871 and 1886 (Agurajuja and Wood, 2003). There have been further discoveries of this species on the island of Kaua'i. Another population of approximately 60 individuals was discovered in 2010 and a fence was built around the population for protection (K. Wood, pers. comm.). No additional rediscoveries of presumed extinct ferns have been reported, but it is difficult, if not impossible, to know with certainty when a species is definitely extinct. As Palmer (2003) suggested, the presumed extinct fern, *Sceptridium subbifoliatum*, may be overlooked in the field due to the similarity of its young leaves to those of *Marattia douglassii* (Marattiaceae).

Hawaiian ferns and lycophytes are important components in native Hawaiian ecosystems and it is therefore necessary that these plants be better understood and protected. We hope this publication along with the interactive key will evoke interest and further educate those interested in Hawaiian ferns and lycophytes.

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APPENDIX 1. Checklist for the native and naturalized ferns and lycophytes of the Hawaiian Islands. The checklist follows the linear sequence for extant ferns and lycophytes by Christenhusz *et al.* (2011) with several modifications (Rothfels *et al.*, 2012b).

^E endemic; ^I indigenous; ^{NZ} naturalized

Hawaiian Island abbreviations: N=Ni'ihau; K=Kaua'i; O=O'ahu; Mo=Moloka'i; L=Lāna'i; Ma=Maui; Ka=Kaho'olawe; H=Hawai'i

(ex)=extinct

* synonyms listed are those that represent updates subsequent to Palmer (2003)

LYCOPHYTES

1. *Lycopodiaceae* P. Beauv. ex Mirb.

Huperzia Bernh.

^E *Huperzia erosa* Beitel & W. H. Wagner

Distribution: K/O/Mo/L/Ma/H

^I *Huperzia erubescens* (Brack.) Holub

Distribution: K/O/Mo/Ma/H

^I *Huperzia filiformis* (Sw.) Holub

Distribution: K/O/Mo/L/Ma/H

^I *Huperzia haleakalae* (Brack.) Holub

Distribution: Ma (ex)

^E *Huperzia mannii* (Hillebr.) Kartesz & Gandhi

Distribution: K (ex)/Ma/H

^E *Huperzia nutans* (Brack.) Rothm.

Distribution: K (ex)/O

^I *Huperzia phyllantha* (Hook. & Arn.) Holub

Distribution: K/O/Mo/L/Ma/H

^I *Huperzia serrata* (Thunb. ex Murray) Trevis.

Distribution: K/O/Mo/L/H

^E *Huperzia stemmermanniae* (A. C. Medeiros, W. H. Wagner & Hobdy) Kartesz

Distribution: Ma/H

^E *Huperzia subintegra* (Hillebr.) Beitel & W. H. Wagner

Distribution: K/O/Mo/Ma

Lycopodiella Holub

^I *Lycopodiella cernua* (L.) Pic. Serm.

Distribution: K/O/Mo/L/Ma/H

Lycopodium* L.**^ILycopodium venustum* Gaudich. var. *venustum***

Distribution: K/O/Mo/L/Ma/H

^E***Lycopodium venustum* Gaudich. var. *verticale* W. H. Wagner**

Distribution: H

2. **Isoëtaceae** Reichenb.***Isoëtes* L.**^E***Isoëtes hawaiiensis* W. C. Taylor & W. H. Wagner**

Distribution: Ma/H

3. **Selaginellaceae** Willk.***Selaginella* P. Beauv.**^I***Selaginella arbuscula* (Kaulf.) Spring**

Distribution: K/O/Mo/L/Ma/H

note: Selaginella arbuscula was previously considered an endemic species. This species has a greater distribution, occurring in the Society Islands, Ualan, Santa Cruz Island (Vanikoro), and the Marquesas Islands (Hassler and Swale, 2003).

^E***Selaginella deflexa* Brack.**

Distribution: K/O/Mo/Ma/H

^{NZ}***Selaginella kraussiana* (Kunze) A. Braun**

Distribution: O/Ma/H

^{NZ}***Selaginella stellata* Spring**

Distribution: H

^{NZ}***Selaginella umbrosa* Lem. ex Hieron.**

Distribution: H

FERNS

1. **Ophioglossaceae** Martinov***Sceptridium* Lyon**^E***Sceptridium subbifoliatum* (Brack.) Lyon**

Distribution: K (ex)/O (ex)/Mo (ex)/L (ex)/Ma (ex)/H (ex)

Ophioderma* (Blume) Endl.**Ophioderma pendulum* (L.) C. Presl**^I subsp. ***falcatum* (C. Presl) R. T. Clausen**

Distribution: K/O/Mo/L/Ma/H

^I subsp. *pendulum*

Distribution: O/Mo/Ma/H

Ophioglossum L.

^I*Ophioglossum nudicaule* L. f.

Distribution: K/O/H

^I*Ophioglossum petiolatum* Hook.

Distribution: K/O/Mo/L/Ma/H

^I*Ophioglossum polyphyllum* A. Braun

Distribution: K/O/Mo/L (ex)/Ka/Ma/H

2. *Psilotaceae* J.W.Griff. & Henfr.

Psilotum Sw.

^I*Psilotum complanatum* Sw.

Distribution: K/O/Mo/L/Ma/H

^I*Psilotum nudum* (L.) P. Beauv.

Distribution: N/K/O/Mo/L/Ka/Ma/H

3. *Marattiaceae* Kaulf.

Angiopteris Hoffm.

^{NZ} *Angiopteris evecta* (G. Forst.) Hoffm.

Distribution: K/O/Mo/L/Ma/H

Marattia Sw.

^E *Marattia douglasii* (C. Presl) Baker

Distribution: K/O/Mo/L/Ma/H

4. *Hymenophyllaceae* Mart.

Callistopteris Copel.

^E *Callistopteris baldwinii* (D. C. Eaton) Copel.

Distribution: K/O/Mo/L/Ma/H

Crepidomanes C. Presl

^E *Crepidomanes draytonianum* (Brack.) Ebihara & K. Iwats.

Syn. *Vandenboschia draytoniana* (Brack.) Copel.

Distribution: K/O/Mo/L/Ma/H

^I*Crepidomanes minutum* (Blume) K. Iwats.

Syn. *Gonocormus minutus* (Blume) Bosch

Distribution: K/O/Mo/L/Ma/H

¹***Crepidomanes proliferum*** (Blume) BostockSyn. *Gonocormus prolifer* (Blume) Prantl

Distribution: Ma/H

Hymenophyllum Sm.^E ***Hymenophyllum lanceolatum*** Hook. & Arn.Syn. *Sphaerocionium lanceolatum* (Hook. & Arn.) Copel.

Distribution: K/O/Mo/L/Ma/H

^E ***Hymenophyllum obtusum*** Hook. & Arn.Syn. *Sphaerocionium obtusum* (Hook. & Arn.) Copel.

Distribution: O/Mo/L/Ma/H

^E ***Hymenophyllum recurvum*** Gaudich.Syn. *Mecodium recurvum* (Gaudich.) Copel.

Distribution: K/O/Mo/L/Ma/H

Vandenboschia Copel.^E ***Vandenboschia cyrtotheca*** (Hillebr.) Copel.

Distribution: K/O/Mo/L/Ma/H

^E ***Vandenboschia davallioides*** (Gaudich.) Copel.

Distribution: K/O/Mo/L/Ma/H

^E ***Vandenboschia tubiflora*** F. S. Wagner

Distribution: K

5. **Gleicheniaceae** C. Presl***Dicranopteris*** Bernh.***Dicranopteris linearis*** (Burm. f.) Underw.

Distribution: K/O/Mo/L/Ma/H

Diplopterygium (Diels) Nakai^E ***Diplopterygium pinnatum*** (Kunze) Nakai

Distribution: K/O/Mo/L/Ma/H

Sticherus C. Presl^E ***Sticherus owbyhensis*** (Hook.) Ching

Distribution: K/O/Mo/L/Ma/H

6. **Lygodiaceae** M. Roem.***Lygodium*** Sw.^{NZ} ***Lygodium japonicum*** (Thunb.) Sw.

Distribution: O/H

7. **Schizaeaceae** Kaulf.

Schizaea Sm.

^E ***Schizaea robusta*** Baker

Distribution: K/O/Mo/L/Ma/H

8. **Marsileaceae** Mirb.

Marsilea L.

^{NZ} ***Marsilea minuta*** L.

Syn. *Marsilea crenata* C. Presl

Distribution: O

^E ***Marsilea villosa*** Kaulf.

Distribution: N/O/Mo

9. **Salviniaceae** Martinov

Salvinia Seg.

^{NZ} ***Salvinia molesta*** D. S. Mitch.

Distribution: O/H

Azolla Lam.

^{NZ} ***Azolla filiculoides*** Lam.

Distribution: K/O/Mo/L/Ma/H

10. **Cibotiaceae** Korall

Cibotium Kaulf.

^E ***Cibotium chamissoi*** Kaulf.

Distribution: O/Mo/L/Ma/H

^E ***Cibotium glaucum*** (Sm.) Hook. & Arn.

Distribution: K/O/Mo/L/Ma/H

^E ***Cibotium menziesii*** Hook.

Distribution: K/O/Mo/L/Ma/H

^E ***Cibotium nealiae*** O. Deg.

Distribution: K

11. **Cyatheaceae** Kaulf.

Sphaeropteris Bernh.

^{NZ} ***Sphaeropteris cooperi*** (Hook. ex F. Muell.) R. M. Tryon

Distribution: K/O/L/Ma/H

12. **Dicksoniaceae** M.R. Schomb.**Dicksonia** L'Hér.^{NZ} **Dicksonia fibrosa** Colenso

Distribution: H

13. **Lindsaeaceae** C. Presl ex M.R. Schomb.**Lindsaea** Dryand. ex Sm.^{NZ} **Lindsaea ensifolia** Sw.

Distribution: K/O/Mo/Ma/H

Lindsaea repens (Bory) Thwaites^E var. **macraeana** (Hook. & Arn.) C. Chr.

Distribution: K/O/Mo/L/Ma/H

Sphenomeris Maxon^I **Sphenomeris chinensis** (L.) Maxon

Distribution: K/O/Mo/L/Ma/H

14. **Dennstaedtiaceae** Lotsy**Hypolepis** Bernh.**Hypolepis hawaiiensis** Brownsey^E var. **hawaiiensis**

Distribution: K/O/Mo/L/Ma/H

^E var. **mauiensis** (Hillebr.) D. D. Palmer

Distribution: Ma

Microlepia C. Presl^I **Microlepia speluncae** (L.) T. Moore

Distribution: K/O/Mo/Ma/H

Microlepia strigosa (Thunb.) C. Presl^E var. **mauiensis** (W. H. Wagner) D. D. Palmer

Distribution: Ma/H

^I var. **strigosa**

Distribution: K/O/Mo/L/Ma/H

Pteridium Gled. ex Scop.**Pteridium aquilinum** (L.) Kuhn^E subsp. **decompositum** (Gaudich.) Lamoureux ex J. A. Thomson

Distribution: K/O/Mo/L/Ma/H

15. **Pteridaceae** E. D. M. Kirchn.

***Adiantum* L.**

^{NZ} ***Adiantum 'Edwinii'***

Distribution: O/L/Ma

^I ***Adiantum capillus-veneris* L.**

Distribution: N/K/O/Mo/L/Ma/H

^{NZ} ***Adiantum hispidulum* Sw.**

Distribution: K/O/Mo/L/Ka/Ma/H

^{NZ} ***Adiantum raddianum* C. Presl**

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Adiantum tenerum* Sw.**

Distribution: O/Mo/Ma

***Ceratopteris* Brongn.**

^{NZ} ***Ceratopteris gaudichaudii* Brongn.**

var. ***vulgaris*** Masuyama & Watano

Distribution: K/O/H

***Cheilanthes* Sw.**

^{NZ} ***Cheilanthes viridis* (Forssk.) Sw.**

Distribution: K/O/L/Ma/H

***Coniogramme* Fée**

^E ***Coniogramme pilosa* (Brack.) Hieron.**

Distribution: K/O/Mo/L/Ma/H

***Doryopteris* J. Sm.**

^E ***Doryopteris angelica* K. R. Wood & W. H. Wagner**

Distribution: K

^E ***Doryopteris decipiens* (Hook.) J. Sm.**

Distribution: N/K/O/Mo/L/Ka/Ma/H

^E ***Doryopteris decora* Brack.**

Distribution: K/O/Mo/L/Ka/Ma/H

^E ***Doryopteris takeuchii* (W. H. Wagner) W. H. Wagner**

Distribution: O

***Haplopteris* C. Presl**

^I ***Haplopteris elongata* (Sw.) E. H. Crane**

Distribution: K/O/Mo/L/Ma/H

Pellaea Link^I**Pellaea ternifolia** (Cav.) Link

Distribution: K/O/Mo/L/Ma/H

Pityrogramma Link^{NZ}**Pityrogramma austroamericana** Domin

Distribution: N/K/O/Mo/L/Ka/Ma/H

^{NZ}**Pityrogramma calomelanos** (L.) Link

Distribution: N/K/O/Mo/L/Ka/Ma/H

Pteris L.^I**Pteris cretica** L.

Distribution: K/O/Mo/L/Ma/H

^I**Pteris excelsa** Gaudich.

Distribution: K/O/Mo/L/Ma/H

^E**Pteris hillebrandii** Copel.

Distribution: K/O/Mo/L/Ma/H

^E**Pteris irregularis** Kaulf.

Distribution: K/O/Mo/L/Ma/H

^E**Pteris lidgatei** (Hillebr.) Christ

Distribution: O/Mo/Ma

^{NZ}**Pteris tremula** R. Br.

Distribution: Ma

^{NZ}**Pteris vittata** L.

Distribution: K/O/Mo/L/Ma/H

16. **Cystopteridaceae** (Payer) Shmakov**Cystopteris** Bernh.^E**Cystopteris douglasii** Hook.

Distribution: Ma/H

^E**Cystopteris sandwicensis** Brack.

Distribution: K/O/L/Ma

17. **Aspleniaceae** Newman**Asplenium** L.^E**Asplenium acuminatum** Hook. & Arn.

Distribution: K/O/Mo/L/Ma/H

^I*Asplenium adiantum-nigrum* L.

Distribution: K/O/Mo/L/Ma/H

^I*Asplenium aethiopicum* (Burm. f.) Bech.

Distribution: K/O/Mo/L/Ma/H

^I*Asplenium caudatum* G.Forst.

Syn. *Asplenium horridum* Kaulf. var. *glabratum* (W. J. Rob.) D. D. Palmer; *Asplenium horridum* Kaulf. var. *horridum*

Distribution: K/O/Mo/L/Ma/H

Asplenium contiguum Kaulf.

^E var. *contiguum*

Distribution: K/O/Mo/L/Ma/H

^E var. *hirtulum* C. Chr.

Distribution: K/Ma

^E *Asplenium dielirectum* Viane

Syn. *Diellia erecta* Brack.

Distribution: O/Mo/L (ex)/Ma/H

^E *Asplenium dielfalcatum* Viane

Syn. *Diellia falcata* Brack.

Distribution: O

^E *Asplenium diellaciniatum* Viane

Distribution: K

^E *Asplenium dielmannii* Viane

Syn. *Diellia mannii* (D. C. Eaton) W. J. Rob.

Distribution: K

^E *Asplenium dielpallidum* N. Snow

Syn. *Diellia pallida* W. H. Wagner

Distribution: K

^I*Asplenium excisum* C. Presl

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium haleakalense* W. H. Wagner

Distribution: Ma/H

^E *Asplenium hobdyi* W. H. Wagner

Distribution: K/Mo/Ma/H

^I*Asplenium insiticium* Brack.

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium kaulfussii* Schltdl.

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium leucostegioides* BakerSyn. *Diellia leucostegioides* (Baker) W. H. Wagner

Distribution: Ma (ex)

^I *Asplenium lobulatum* Mett.

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium macraei* Hook. & Grev.

Distribution: K/O/Mo/L/Ma/H

^I *Asplenium monanthes* L.

Distribution: Ma/H

Asplenium nidus L.

Distribution: K/O/Mo/L/Ma/H

^I *Asplenium normale* D. Don

Distribution: K/O/Mo/L/Ma/H

Asplenium peruvianum Desv.^E var. *insulare* (C. V. Morton) D. D. Palmer

Distribution: Ma/H

^I *Asplenium polyodon* G. Forst.

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium schizophyllum* C. Chr.

Distribution: K/H

^E *Asplenium sphenotomum* Hillebr.

Distribution: K/O/Mo/L/Ma/H

Asplenium trichomanes L.^E subsp. *densum* (Brack.) W. H. Wagner

Distribution: Ma/H

^I *Asplenium unilaterale* Lam.

Distribution: K/O/Mo/L/Ma/H

^E *Asplenium unisorum* (W. H. Wagner) VianeSyn. *Diellia unisora* W. H. Wagner

Distribution: O

18. **Thelypteridaceae** Ching ex Pic. Serm.

Cyclosorus Link

^E ***Cyclosorus boydiae*** (D. C. Eaton) W. H. Wagner

Syn. *Christella boydiae* (D.C. Eaton) Holttum

Distribution: O/Ma

^E ***Cyclosorus cyatheoides*** (Kaulf.) Farw.

Syn. *Christella cyatheoides* (Kaulf.) Holttum

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Cyclosorus dentatus*** (Forssk.) Ching

Syn. *Christella dentata* (Forssk.) Brownsey & Jermy

Distribution: K/O/Mo/L/Ma/H

^E ***Cyclosorus hudsonianus*** (Brack.) Ching

Syn. *Pneumatopteris hudsoniana* (Brack.) Holttum

Distribution: K/O/Mo/L/Ma/H

^I ***Cyclosorus interruptus*** (Willd.) H. Itô

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Cyclosorus parasiticus*** (L.) Farw.

Syn. *Christella parasitica* (L.) H. Lév.

Distribution: K/O/Mo/L/Ma/H

^E ***Cyclosorus pendens*** (D. D. Palmer) N. Snow

Syn. *Pneumatopteris pendens* D. D. Palmer

Distribution: K/O/Mo/Ma/H

^E ***Cyclosorus sandwicensis*** (Brack.) Copel.

Syn. *Pneumatopteris sandwicensis* (Brack.) Holttum

Distribution: K/O/Mo/L/Ma/H

^E ***Cyclosorus waialele*** (Flynn) W. H. Wagner

Syn. *Christella waialele* (Flynn) D. D. Palmer

Distribution: K

Macrothelypteris (H. Itô) Ching

^{NZ} ***Macrothelypteris torresiana*** (Gaudich.) Ching

Distribution: K/O/Ma/H

Pseudophegopteris Ching

^E ***Pseudophegopteris keraudreniana*** (Gaudich.) Holttum

Distribution: K/O/Mo/L/Ma/H

Thelypteris Schmidel^E ***Thelypteris globulifera*** (Brack.) C. F. ReedSyn. *Amauropelta globulifera* (Brack.) Holttum

Distribution: K/O/Mo/L/Ma/H

19. **Blechnaceae** Newman***Blechnum*** L.^{NZ} ***Blechnum appendiculatum*** Willd.

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Blechnum orientale*** L.

Distribution: O

Doodia R. Br.^E ***Doodia kunthiana*** Gaudich.

Distribution: K/O/Mo/L/Ma/H

^E ***Doodia lyonii*** O. Deg.

Distribution: K/O/Ma/H (ex)

Sadleria Kaulf.^E ***Sadleria cyatheoides*** Kaulf.

Distribution: K/O/Mo/L/Ma/H

^E ***Sadleria pallida*** Hook. & Arn.

Distribution: K/O/Mo/L/Ma/H

^E ***Sadleria souleyetiana*** (Gaudich.) T. Moore

Distribution: K/O/Mo/L/Ma/H

^E ***Sadleria squarrosa*** (Gaudich.) T. Moore

Distribution: K/O/Mo/L/Ma/H

^E ***Sadleria unisora*** (Baker) W. J. Rob.

Distribution: K

^E ***Sadleria wagneriana*** D. D. Palmer & Flynn

Distribution: K

20. **Athyriaceae** Alston***Athyrium*** Roth^E ***Athyrium microphyllum*** (Sm.) Alston

Distribution: K/O/Mo/L/Ma/H

Deparia Hook. & Grev.^E ***Deparia cataracticola*** M. Kato

Distribution: K

^E ***Deparia fenzliana*** (Lueress.) M. Kato

Distribution: K/O/Mo/L/Ma/H

^E ***Deparia kaalaana*** (Copel.) M. Kato

Distribution: K (ex)/Ma (ex)/H (ex)

^E ***Deparia marginalis*** (Hillebr.) M. Kato

Distribution: K/Mo/L/Ma/H

^{NZ} ***Deparia petersenii*** (Kunze) M. Kato

Distribution: K/O/Mo/L/Ma/H

^E ***Deparia prolifera*** (Kaulf.) Hook. & Grev.

Distribution: K/O/Mo/L/Ma/H

Diplazium Sw.^E ***Diplazium arnottii*** Brack.

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Diplazium esculentum*** (Retz.) Sw.

Distribution: K/O/Mo/L/Ma/H

^E ***Diplazium molokaiense*** W. J. Rob.

Distribution: K (ex)/O (ex)/Mo (ex)/L (ex)/Ma

^E ***Diplazium sandwichianum*** (C. Presl) Diels

Distribution: K/O/Mo/L/Ma/H

21. **Dryopteridaceae** Herter***Arachniodes*** Blume^E ***Arachniodes insularis*** W. H. Wagner

Distribution: K/O/Mo/Ma/H

Ctenitis (C. Chr.) C. Chr.^E ***Ctenitis latifrons*** (Brack.) Copel.

Distribution: K/O/Mo/L/Ma/H

^E ***Ctenitis squamigera*** (Hook. & Arn.) Copel.

Distribution: K/O/Mo/L/Ma

Cyrtomium C. Presl^I ***Cyrtomium caryotideum*** (Wall. ex Hook. & Grev.) C. Presl

Distribution: K/O/Mo/L/Ma/H

^{NZ} *Cyrtomium falcatum* (L. f.) C. Presl

Distribution: K/O/Mo/L/Ma/H

Dryopteris Adans.

Dryopteris crinalis (Hook. & Arn.) C. Chr.

^E var. *crinalis*

Distribution: K/O/Mo/L/Ma/H

^E var. *podosora* (W. H. Wagner) D. D. Palmer

Distribution: K

Dryopteris fuscoatra (Hillebr.) W. J. Rob.

^E var. *fuscoatra*

Distribution: K/O/Mo/L/Ma/H

^E var. *lamoureuxii* Fraser-Jenk.

Distribution: Ma

Dryopteris glabra (Brack.) Kuntze

^E var. *alboviridis* (W. H. Wagner) D. D. Palmer

Distribution: K

^E var. *flynnii* D. D. Palmer

Distribution: K

^E var. *glabra*

Distribution: K/O/Mo/L/Ma/H

^E var. *hobdyana* (W. H. Wagner) D. D. Palmer

Distribution: Ma

^E var. *nuda* (Underw.) Fraser-Jenk.

Distribution: K/O/Mo/Ma

^E var. *pusilla* (Hillebr.) Fraser-Jenk.

Distribution: K

^E var. *soripes* (Hillebr.) Herat ex Fraser-Jenk.

Distribution: K/O/Mo/Ma/H

^E *Dryopteris hawaiiensis* (Hillebr.) W. J. Rob.

Distribution: K/O/Mo/Ma/H

^E *Dryopteris mauiensis* C. Chr.

Distribution: K/O/Mo/L/Ma/H

^E *Dryopteris rubiginosa* (Brack.) KuntzeSyn. *Nothoperanema rubiginosum* (Brack.) A.R. Sm. & D. D. Palmer

Distribution: K/O/Mo/L/Ma/H

^E *Dryopteris sandwicensis* (Hook. & Arn.) C. Chr.

Distribution: K/O/Mo/L/Ma/H

^E *Dryopteris subbipinnata* W. H. Wagner & Hobdy

Distribution: Ma/H

^E *Dryopteris tetrapinnata* W. H. Wagner & Hobdy

Distribution: Ma

Dryopteris unidentata (Hook. & Arn.) C. Chr.^E var. *paleacea* (Hillebr.) Herat ex Fraser-Jenk.

Distribution: K/O/Mo/Ma/H

^E var. *unidentata*

Distribution: K/O/Mo/L/Ma/H

^I *Dryopteris wallichiana* (Spreng.) Hyl.

Distribution: K/O/Mo/Ma/H

Elaphoglossum Schott ex J. Sm.^E *Elaphoglossum aemulum* (Kaulf.) Brack.

Distribution: K/O/Mo/L/Ma/H (ex)

^E *Elaphoglossum alatum* Gaudich.

Distribution: O

^E *Elaphoglossum crassicaule* Copel.

Distribution: K

^E *Elaphoglossum crassifolium* (Gaudich.) W. R. Anderson & Crosby

Distribution: K/O/Mo/L/Ma/H

^E *Elaphoglossum fauriei* Copel.

Distribution: O/Mo

^I *Elaphoglossum paleaceum* (Hook. & Grev.) Sledge

Distribution: K/O/Mo/L/Ma/H

^E *Elaphoglossum parvisquameum* Skottsb.

Distribution: Mo/L/Ma/H

^E *Elaphoglossum pellucidum* Gaudich.

Distribution: K/O/Mo/Ma/H

^E *Elaphoglossum wawrae* (Luer ss.) C. Chr.

Distribution: K/O/Mo/Ma/H

***Polystichum* Roth**

^E *Polystichum bonseyi* W. H. Wagner & Hobdy

Distribution: Ma/H

^E *Polystichum haleakalense* Brack.

Distribution: Ma/H

^E *Polystichum hillebrandii* Carruth.

Distribution: Ma/H

22. **Nephrolepidaceae** Pic. Serm.

***Nephrolepis* Schott**

^{NZ} *Nephrolepis brownii* (Desv.) Hovenkamp & Miyam.

Syn. *Nephrolepis multiflora* (Roxb.) F. M. Jarrett ex C. V. Morton

Distribution: N/K/O/Mo/L/Ka/Ma/H

^I *Nephrolepis cordifolia* (L.) C. Presl

Distribution: K/O/Mo/L/Ma/H

^E *Nephrolepis exaltata* (L.) Schott subsp. *hawaiiensis* W. H. Wagner

Distribution: N/K/O/Mo/L/Ma/H

^{NZ} *Nephrolepis falcata* (Cav.) C. Chr. '*Furcans*'

Distribution: K/O/Mo/L/Ma/H

^{NZ} *Nephrolepis hirsutula* (G. Forst.) C. Presl '*Superba*'

Distribution: K/Ma

23. **Tectariaceae** Panigrahi

***Tectaria* Cav.**

^E *Tectaria gaudichaudii* (Mett.) Maxon

Distribution: K/O/Mo/L/Ma/H

^{NZ} *Tectaria incisa* Cav.

Distribution: K/O/Ma/H

24. **Davalliaceae** M. R. Schomb. ex A. B. Frank

***Davallia* Sm.**

^{NZ} *Davallia fejeensis* Hook.

Distribution: O/Ma

25. **Polypodiaceae** Bercht. & J. Presl***Adenophorus* Gaudich.**^E ***Adenophorus abietinus*** (D. C. Eaton) K. A. Wilson

Distribution: K/O/L/Ma

^E ***Adenophorus epigaeus*** (L. E. Bishop) W. H. Wagner

Distribution: K

^E ***Adenophorus haalilioanus*** (Brack.) K. A. Wilson

Distribution: K/O

^E ***Adenophorus hymenophylloides*** (Kaulf.) Hook. & Grev.

Distribution: K/O/Mo/L/Ma/H

^E ***Adenophorus oahuensis*** (Copel.) L. E. Bishop

Distribution: O

^E ***Adenophorus periens*** L. E. Bishop

Distribution: K/O (ex)/Mo/L (ex)/Ma (ex)/H

Adenophorus pinnatifidus* Gaudich.**^E var. ***pinnatifidus

Distribution: K/O/Mo/L/Ma/H

^E var. ***rockii*** (Copel.) D. D. Palmer

Distribution: K/O/Mo/Ma

Adenophorus tamariscinus* (Kaulf.) Hook. & Grev.**^E var. ***montanus (Hillebr.) L. E. Bishop

Distribution: Mo/Ma/H

^E var. ***tamariscinus***

Distribution: K/O/Mo/L/Ma/H

^E ***Adenophorus tenellus*** (Kaulf.) RankerSyn. *Grammitis tenella* Kaulf.

Distribution: K/O/Mo/L/Ma/H

^E ***Adenophorus tripinnatifidus* Gaudich.**

Distribution: K/O/Mo/L/Ma/H

Lepisorus* (J. Sm.) Ching**¹ ***Lepisorus thunbergianus (Kaulf.) Ching

Distribution: K/O/Mo/L/Ma/H

Microsorium* Link**Microsorium spectrum*** (Kaulf.) Copel.

^E var. ***pentadactylum*** (Hillebr.) D. D. Palmer

Distribution: K/Ma

^E var. ***spectrum***

Distribution: K/O/Mo/L/Ma/H

Oreogrammitis Copel.

^E ***Oreogrammitis baldwinii*** (Baker) Parris

Syn. *Grammitis baldwinii* (Baker) Copel.

Distribution: K

^E ***Oreogrammitis forbesiana*** (W. H. Wagner) Parris

Syn. *Grammitis forbesiana* W. H. Wagner

Distribution: K/Mo/Ma

^E ***Oreogrammitis hookeri*** (Brack.) Parris

Syn. *Grammitis hookeri* (Brack.) Copel.

Distribution: K/O/Mo/L/Ma/H

note: Oreogrammitis hookeri was previously thought to be an indigenous species, but is now considered as distinct from species found in Fiji and American Samoa (B. Parris, pers. comm.)

Phlebodium (R. Br.) J. Sm.

^{NZ} ***Phlebodium aureum*** (L.) J. Sm.

Distribution: K/O/Mo/L/Ma/H

Phymatosorus Pic. Serm.

^{NZ} ***Phymatosorus grossus*** (Langsd. & Fisch.) Brownlie

Distribution: K/O/Mo/L/Ma/H

^{NZ} ***Phymatosorus scolopendria*** (Burm. f.) Pic. Serm.

Distribution: Ma

Platycterium Desv.

^{NZ} ***Platycterium bifurcatum*** (Cav.) C. Chr.

Distribution: O/Ma/H

^{NZ} ***Platycterium superbum*** de Jonch. & Hennipman

Distribution: O

Polypodium L.

Polypodium pellucidum Kaulf.

^E var. ***acuminatum*** D. D. Palmer

Distribution: K/Ma

^E var. *pellucidum*

Distribution: K/O/Mo/L/Ma/H

^E var. *vulcanicum* Skottsb.

Distribution: Mo/Ma/H

Pyrrosia Mirb.

^{NZ} *Pyrrosia piloselloides* (L.) M. G. Price

Distribution: O

Stenogrammitis Labiak

^E *Stenogrammitis saffordii* (Maxon) Labiak

Syn. *Lellingeria saffordii* (Maxon) A. R. Sm. & R. C. Moran

Distribution: K/O/Mo/L/Ma/H

APPENDIX 2. Estimated origins of 78 Hawaiian fern and lycophyte taxa based on molecular phylogenetic studies and/or geographical distributions.

^E endemic; ^I indigenous
* = origin inferred based on distribution of genus or species

Status	Taxa	Distribution of lineage sister to Hawaiian Lineage	References
Ferns			
E	<i>Adenophorus</i> - 10 species	Neotropics	Ranker <i>et al.</i> , 2004
E	<i>Arachniodes insularis</i>	Asia	*
E	<i>Asplenium acuminatum</i>	unknown	
E	<i>Asplenium contiguum</i>	unknown	
E	<i>Asplenium haleakalense</i>	unknown	
E	<i>Asplenium hobdyi</i>	Paleotropics	Schneider <i>et al.</i> , 2005
E	<i>Asplenium kaulfussii</i>	unknown	
E	<i>Asplenium leucostegioides</i>	unknown	
E	<i>Asplenium macraei</i>	unknown	
E	<i>Asplenium peruvianum</i> var. <i>insulare</i>	Neotropics	*
E	<i>Asplenium schizophyllum</i>	unknown	
E	<i>Asplenium sphenotomum</i>	unknown	
E	<i>Asplenium trichomanes</i> var. <i>densum</i>	Cosmopolitan	*
E	<i>Asplenium unisorum</i>	unknown	
E	<i>Athyrium microphyllum</i>	unknown	
E	<i>Callistopteris baldwinii</i>	Asia/Indopacific	*
E	<i>Cibotium</i> - 4 species	Neotropics	Geiger <i>et al.</i> , 2007
E	<i>Coniogramme pilosa</i>	Asia/Indopacific	*
E	<i>Crepidomanes draytonianum</i>	unknown	
E	<i>Ctenitis latifrons</i>	unknown	
E	<i>Ctenitis squamigera</i>	unknown	
E	<i>Cyclosorus boydiae</i>	unknown	
E	<i>Cyclosorus cyatheoides</i>	unknown	
E	<i>Cyclosorus hudsonianus</i>	unknown	
E	<i>Cyclosorus pendens</i>	unknown	
E	<i>Cyclosorus sandwicensis</i>	unknown	
E	<i>Cyclosorus waialele</i>	unknown	
E	<i>Cystopteris douglasii</i>	unknown	
E	<i>Cystopteris sandwicensis</i>	unknown	
E	<i>Deparia cataracticola</i>	Asia	*
E	<i>Deparia fenzliana</i>	Asia	*
E	<i>Deparia kaalaana</i>	unknown	
E	<i>Deparia marginalis</i>	unknown	
E	<i>Deparia prolifera</i>	unknown	
E	<i>Diellia</i> clade of <i>Asplenium</i> (6 spp.)	Paleotropics	Schneider <i>et al.</i> , 2005
E	<i>Diplazium arnottii</i>	unknown	
E	<i>Diplazium molokaiense</i> *	unknown	
E	<i>Diplazium sandwichianum</i>	unknown	
E	<i>Diplopterygium pinnatum</i>	Asia/Indopacific	Ranker <i>et al.</i> , unpub. data
E	<i>Doodia kunthiana</i>	Indopacific	*
E	<i>Doodia lyonii</i>	Indopacific	*
E	<i>Doryopteris angelica</i>	unknown	
E	<i>Doryopteris decipiens</i>	unknown	

APPENDIX 2. Continued.

Status	Taxa	Distribution of lineage sister to Hawaiian Lineage	References
E	<i>Doryopteris decora</i>	unknown	
E	<i>Doryopteris subdecipiens</i>	unknown	
E	<i>Doryopteris takeuchii</i>	unknown	
E	<i>Dryopteris crinalis</i> , <i>D. mauliensis</i> , <i>D. sandwicensis</i> , <i>D. tetrapinnata</i> , <i>D. unidentata</i>	Asia	Geiger and Ranker, 2005
E	<i>Dryopteris fusco-atra</i>	Asia	Geiger and Ranker, 2005
E	<i>Dryopteris glabra</i> + <i>D. hawaiiensis</i>	Asia	Geiger and Ranker, 2005
E	<i>Dryopteris rubiginosa</i>	Asia	Geiger and Ranker, 2005
E	<i>Dryopteris subbipinnata</i> (sister to <i>D. wallichiana</i>)	Pantropical	Geiger and Ranker, 2005
E	<i>Elaphoglossum aemulum</i>	unknown	
E	<i>Elaphoglossum alatum</i>	unknown	
E	<i>Elaphoglossum crassicaule</i>	unknown	
E	<i>Elaphoglossum crassifolium</i>	unknown	
E	<i>Elaphoglossum fauriei</i>	unknown	
E	<i>Elaphoglossum parvisquameum</i>	unknown	
E	<i>Elaphoglossum pellucidum</i>	unknown	
E	<i>Elaphoglossum wawrae</i>	unknown	
E	<i>Hymenophyllum lanceolatum</i>	Indopacific	Ebihara <i>et al.</i> , 2004; Hennequin <i>et al.</i> , 2003, 2006; Pryer <i>et al.</i> , 2001
E	<i>Hymenophyllum obtusum</i>	unknown	
E	<i>Hymenophyllum recurvum</i>	unknown	
E	<i>Hypolepis hawaiiensis</i>	Austral	Ranker <i>et al.</i> , unpub. data
E	<i>Lindsaea repens</i> var. <i>macraeana</i>	Asia/Indopacific	*
E	<i>Marattia douglasii</i>	Neotropics	Murdock, 2008
E	<i>Marsilea villosa</i>	North America/Neotropics	Whitten <i>et al.</i> , 2012
E	<i>Microsorium spectrum</i>	Asia	Kreier <i>et al.</i> , 2008
E	<i>Nephrolepis exaltata</i> subsp. <i>hawaiiensis</i>	Pantropical	*
E	<i>Oreogrammitis baldwinii</i> , <i>O. forbesiana</i> , <i>O. hookeri</i>	Asia/Indopacific	Ranker <i>et al.</i> , 2004
E	<i>Polypodium pellucidum</i>	Boreal	Haufler and Ranker, 1995
E	<i>Polystichum bonseyi</i> + <i>P. haleakalense</i>	Asia	Driscoll and Barrington, 2007
E	<i>Polystichum hillebrandii</i>	Asia	Driscoll and Barrington, 2007
E	<i>Pseudophegopteris keraudreniana</i>	Asia	*
E	<i>Pteris hillebrandii</i>	unknown	
E	<i>Pteris irregularis</i>	unknown	
E	<i>Pteris lydgatei</i>	unknown	
E	<i>Sadleria</i> - 6 species	unknown	
E	<i>Sceptridium subbifoliatum</i> *	unknown	
E	<i>Schizaea robusta</i>	unknown	
E	<i>Stenogrammitis saffordii</i>	Neotropics	Sundue <i>et al.</i> , 2010
E	<i>Sticherus owhyhensis</i>	unknown	
E	<i>Tectaria gaudichaudii</i>	unknown	
E	<i>Thelypteris globulifera</i>	unknown	
E	<i>Vandenboschia cyrtotheca</i>	unknown	

APPENDIX 2. Continued.

Status	Taxa	Distribution of lineage sister to Hawaiian Lineage	References
E	<i>Vandenboschia davallioides</i>	unknown	
E	<i>Vandenboschia tubiflora</i>	unknown	
I	<i>Adiantum capillus-veneris</i>	Cosmopolitan	*
I	<i>Asplenium adiantum-nigrum</i>	Paleotropics	*
I	<i>Asplenium aethiopicum</i>	Pantropical	*
I	<i>Asplenium caudatum</i>	Asia/Indopacific	*
I	<i>Asplenium excisum</i>	Asia/Indopacific	*
I	<i>Asplenium insiticium</i>	Indopacific	*
I	<i>Asplenium lobulatum</i>	Asia/Indopacific	*
I	<i>Asplenium monanthes</i>	Pantropical	*
I	<i>Asplenium nidus</i>	Paleotropics	*
I	<i>Asplenium normale</i>	Paleotropics	*
I	<i>Asplenium polyodon</i>	Paleotropics	*
I	<i>Asplenium unilaterale</i>	Paleotropics	*
I	<i>Crepidomanes minutum</i>	Asia	*
I	<i>Crepidomanes proliferum</i>	Asia/Indopacific	*
I	<i>Cyclosorus interruptus</i>	Pantropical	*
I	<i>Cyrtomium caryotideum</i>	Asia	*
I	<i>Dicranopteris linearis</i>	Paleotropics	*
I	<i>Dryopteris wallichiana</i>	Pantropical	*
I	<i>Elaphoglossum paleaceum</i>	Neotropics	*
I	<i>Haplopteris elongata</i>	Paleotropics	*
I	<i>Lepisorus thunbergianus</i>	Asia/Indopacific	*
I	<i>Lindsaea repens</i>	Paleotropics	*
I	<i>Microlepia speluncae</i>	Paleotropics	*
I	<i>Microlepia strigosa</i>	Paleotropics	*
I	<i>Nephrolepis cordifolia</i>	Pantropical	*
I	<i>Ophioderma pendulum</i>	Paleotropics	*
I	<i>Ophioglossum nudicaule</i>	Pantropical	*
I	<i>Ophioglossum petiolatum</i>	Pantropical	*
I	<i>Ophioglossum polyphyllum</i>	Paleotropics	*
I	<i>Pellaea ternifolia</i>	Neotropics	*
I	<i>Psilotum complanatum</i>	Pantropical	*
I	<i>Psilotum nudum</i>	Pantropical	*
I	<i>Pteridium aquilinum</i>	North America	Der <i>et al.</i> , 2009
I	<i>Pteris cretica</i>	Cosmopolitan	*
I	<i>Pteris excelsa</i>	Paleotropics	*
I	<i>Sphenomeris chinensis</i>	Paleotropics	*
I	<i>Tectaria incisa</i>	Neotropics	*
Lycophytes			
E	<i>Huperzia erosa</i>	unknown	
E	<i>Huperzia mannii</i>	unknown	
E	<i>Huperzia nutans</i>	unknown	
E	<i>Huperzia stemmermanniae</i>	unknown	
E	<i>Huperzia subintegra</i>	unknown	
E	<i>Isoëtes hawaiiensis</i>	Boreal	Hoot <i>et al.</i> , 2006
E	<i>Selaginella deflexa</i>	unknown	
I	<i>Selaginella arbuscula</i>	South Pacific	*
I	<i>Huperzia erubescens</i>	Asia	*

APPENDIX 2. Continued.

Status	Taxa	Distribution of lineage sister to Hawaiian Lineage	References
I	<i>Huperzia filiformis</i>	Tropical America	*
I	<i>Huperzia haleakalae</i>	Boreal	*
I	<i>Huperzia phyllantha</i>	Asia/Indopacific	*
I	<i>Huperzia serrata</i>	Asia	*
I	<i>Lycopodiella cernua</i>	Pantropical	*
I	<i>Lycopodium venustum</i>	South Pacific	*